SOME ASPECTS OF LEARNING IN INSECTS.

by

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SUMMARY

The behaviour of two species of insect - the cockroach Nauphoeta cinerea and the honey-bee Apis mellifica - was examined in a number of learning situations. An attempt was made to relate the results to other comparative studies of learning; to theories of discrimination learning; and to the life history of the animals concerned.

A: Nauphoeta cinerea.

1) In preliminary experiments attempts were made to find reinforcers for the cockroach and to design suitable apparatus. It was found that:

a) escape from bright light was not a reliable way of reinforcing maze running behaviour.

b) the cockroach would not learn to run a maze for food or water reward, even after considerable periods of deprivation.

c) the cockroach would learn a maze problem to avoid electric shock. Mazes were designed in which the cockroach could learn a simple positional discrimination with maximal efficiency.

2) It was found that cockroaches very quickly learn an active avoidance of a place in which they have been punished. Frequently, a major change in behaviour occurred after only one trial.

3) It was shown that cockroaches could easily learn to discriminate between the two arms of a Y-maze on the basis of odour, light or air current cues.

4) The behaviour of the cockroach was examined in a 'shuttlebox', a complex avoidance situation intensively studied with mammalian species. Up to a point, the behaviour of the cockroach was similar to that of higher animals but the cockroaches were not able to completely solve the problem.

5) In a multi-reversal situation cockroaches do not improve as a function of reversal experience. Discrimination reversal learning has been widely studied in a great variety of animals and the behaviour of the cockroach is compared with that of other species.

6) The role of avoidance learning was examined in a natural situation. Avoidance learning seems to be of prime importance in learning to avoid territorial areas.

B: Apis mellifica

1) Preliminary experiments established techniques for training bees.

2) In a multi-reversal of a visual discrimination bees show a steady deterioration in performance. This behaviour is related to the life history of the bee .

3) Concept formation was examined in the bee. Recently, claims have been made that bees are capable of very high levels of visual concept formation. In general, these claims were refuted and earlier 'flicker' theories of bee vision re-affirmed. However, this theory is not wholly adequate.

The results are discussed and concepts of 'learning ability' and 'evolution of intelligence' current in comparative psychology critiscised.

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1.

INTRODUCTION.

In this introduction I shall attempt to describe the viewpoint which led me to look at particular aspects of learning in particular insects. Much of my research was influenced by ideas current in comparative psychology. I shall first describe some ideas in this field.

The theme of many studies in the comparative psychology of learning has been that of 'intelligence' or 'learning capacity' and the possibility of tracing the evolution of this property from the simplest animals to the most complex. An eventual outcome of this kind of research might be stated as the possibility that "simple as well as complex learning tasks might be arranged into an orderly classification in terms of difficulty, and the capabilities of animals on these tasks would correspond roughly to their positions on the phylogenetic scale" (Harlow 1958). Although such concepts as 'intelligence' and 'learning capacity' remain undefined, there now exists a considerable body of comparative data on the performance of different species on particular learning tasks.

One man whose name is particularly linked with this kind of approach is M.E. Bitterman. He has concentrated his attention on two kinds of learning task; probability learning and multi-reversal learning, as he claims these tests show up inter-species differences in learning ability. He and his students / .....

/ students have studied the behaviour of rats, pigeons, fish, turtles, crabs, cockroaches and worms in these learning situations.

In general, his experiments run along the following lines. Firstly, he takes an animal and finds some way to motivate it. How this is done will depend upon the particular species under investigation. In his experiments with fish the animals were deprived of food and rewarded with mealworms; with crabs the reward was escape from immersion in distilled water. He then offers the animal a choice of two responses, A and B, only one of which produces the reward. Fish had a choice of pushing one of two buttons with their heads; crabs had a choice of climbing up into one of two arms of a T-maze.

In the probability learning situation the alternative carrying reward varies from trial to trial. In a typical experiment alternative A would be rewarded on, say, a random 70 per cent of the trials and B would be rewarded the other 30 per cent. Thus it can never be predicted which of the two responses will be rewarded on any particular trial, only the ratio of reinforcement is fixed. Two types of response patteern have been observed in this situation. 'Maximising' is said to occur when the animal consistently carries out the most frequently rewarded response. Thus in the example above the animal would carry out alternative A 100 per cent of the time. 'Matching' refers to the distribution of responses to the stimuli in proportion approximating the ratio of reinforcement. In the example above the animal would carry out A 70 per cent of the time and B 30 per cent of the time. Maximising is the / .....

TABLE ONE.

REVERSAL LEARNING.

Animal tested.	Behaviour observed.	Reference.
Monkey.	Improves.	Warren 1965.
Rat.	Improves.	North 1950.
Pigeon.	Improves.	Bullock & Bitterman 1962a.
Turtle.	No improvement.[1]	Kirke & Bitterman 1963.
Fish.	No improvement.	Wodinsky & Bitterman 1957.
Cockroach.	Slight improvement.[2]	Longo 1964.
Crab.	No improvement.	Datta, Milstein & Bitterman 1960.
Earthworm.	Slight improvement.[2]	Datta 1962.
Octopus.	Improves.	Mackintosh 1965a.
Isopod.	Improves.[3]	Morrow & Smithson 1969.

PROBABILITY LEARNING.

Animal tested.	Behaviour observed.	Reference.
Monkey.	Maximises.	Wilson & Rollin 1959.
Rat.	Maximises.	Bitterman 1963.
Pigeon.	Maximises.	Bullock & Bitterman 1962b.
Turtle.	Matches.[1]	Bitterman 1963.
Fish.	Matches.	Behrend & Bitterman 1963.
Cockroach.	Matches.	Longo 1964.

1: improves and maximises if the cues are spatial e.g. left/right rather than visual.

2: improvement is not a function of reversal experience but of general adaptation to experimental conditions.

3: this result is discussed in the section on reversal learning in the cockroach.

/ the more efficient form of behaviour, given that it is impossible to predict the actual sequence of rewards, this behaviour pattern will result in the animal scoring the maximum number of rewards possible.

In the reversal learning problem, animals are rewarded for choosing alternative A rather than B until a preference for A has been established, then B rather than A is rewarded. When a preference for B has been established, A is again rewarded, and so on for a prescribed number of reversals. Again, two patterns of behaviour have commonly emerged. An animal may relearn late reversals faster than early ones, possibly getting to the stage where it switches over to the other alternative after only one unrewarded choice. In other words, it has 'learnt how to learn' the problem, a form of set learning. Other animals may learn each new reversal at the same rate as the original discrimination. This may imply that the animal is treating each new reversal as a completely new problem, and is transferring nothing from previous solutions.

Both probability and reversal learning have shown up differences between the species tested. Note that the differences described above are not differences in the number of trials taken to learn some thing but qualitative differences in behaviour which, according to Bitterman, reveal that there are different 'laws of learning' in different species (Bitterman 1965). The table opposite shows the behaviour of some animals on these tests, most of the results being contributed by Bitterman / .....

/ Bitterman and his co-workers.

In general it appears that the 'higher' animals all show more efficient solutions to these learning tasks than the lower animals. Monkeys, rats and pigeons show improvement in reversal learning (that is, they learn late reversals faster than early ones), while fish, turtles and all invertebrates tested, except the Octopus, do not. Similarly, the mammals and birds maximise in probability learning situations while sub-mammalian species match.

Bitterman has always insisted that these differences are due to fundamental qualitative differences in the learning processes of the animals concerned. Either an animal is 'rat-like' and shows improvement in reversal learning or it is 'fish-like' and it does not. However, there is now evidence that the differences between these species is one of degree rather than one of kind as suggested by Bitterman. Fish can show a slight improvement in reversal learning (Mackintosh et al 1971) and can perform slightly better than matching on a probability learning task (Mackintosh and Canty 1971). Animals cannot be simply divided into classes but rather show a graded increase in efficiency on these tasks. Rats perform more efficiently than birds, birds perform better than fish and fish better than turtles. Among a series of birds an orderly trend in efficiency on a reversal task has been found. Several species of birds were compared in an identical reversal learning situation. Magpies and mynah birds were found to improve over a series of reversals more than parrots, and / .....

/ and parrots improved far more than pigeons, chickens or quails (Gossetts 1966a, b). Quails showed virtually no improvement at all, while magpies and mynahs were nearly as proficient as rats. In some cases magpies and mynahs showed reversal after only a single unrewarded choice. On the basis of studies of comparative anatomy, magpies, mynahs and parrots have been ranked as 'higher' birds, while quails, pigeons and chickens have been considered to be among the 'lower' birds (Cobb 1960). As well as correlating with taxonomic position, the differences in performance are paralleled by differences in cerebral indices reported for representative species of the same families (Portman and Stingelin 1961).

Despite this reference to comparative anatomy as a measure of 'higher' or'lower' it must be remembered that these terms cannot be clearly defined. There are no truly objective criteria for assessing an animal's position on a 'phylogenetic scale'. Objections have been made to Bitterman's approach on this basis (Hodos and Campbell 1969). However, it is justifiable to use the terms 'higher' and 'lower' if it is realised that the idea of higher and lower levels exists only as a conceptual device to help develop a theory (Schneirla 1949). Our ordering of animals may reflect no more than our subjective feelings about which animals seem more clever or which animals seem closer to man. Doubtless our whole conception of these terms will change as more becomes known about different animals' behaviours; indeed we may have to abandon these terms altogether. The terms

'higher' / .....

/ 'higher' and 'lower' should not be taken to imply that all animals can be classified on a unitary scale.

It could also be argued that the set of differences described so far reflect no more than differences in experimental conditions. Perhaps fish showed little improvement over a series of reversals becuase they were not hungry enough, or too hungry, or some other variable was not quite at the right level. However, a large number of results have now been discussed and it is unlikely that chance alone could have produced such a systematic set of differences. Over a series of reversals, progressive error reduction is greater in monkeys and is successively smaller for rats, passerine birds, non-passerine birds, fish and turtles. Turtles show virtually no error reduction at all.

In general, the studies described so far have been carried out with the same aim as any correlative or comparative method; 'to describe, catalogue, and establish relations among same-level phenomena without recourse to analytical procedures' (Altman 1966). This set of comparative data may also be of help in understanding the mechanisms responsible for the various behaviour patterns seen. A theory which attempts to explain the behaviour of one species in a particular situation should be able to account for differences from other species in terms of differences in the parameters of the proposed theory. Bitterman has attempted to use and extend his experimental methods to theorise about mechanisms underlying the changes in behaviour seen in reversal learning.

Bitterman / .....

Bitterman and his colleagues postulate that improvement in reversal learning results from decrements in retention produced by proactive interference (Gonzalez, Behrend and Bitterman 1967, Lowes and Bitterman 1967). From experiments on human memory it is well known that the learning of X may impair the retention of subsequently learned Y (proactive interference), just as the retention of X may be impaired by the subsequent learning of Y (retroactive interference). Both effects are apparently due to the competition of antagonistic response tendencies; the greater the amount of potentially competing material learned before Y is learned the poorer the retention of Y (underwood 1957).

In Bitterman's studies of reversal learning he invariably given animals one reversal session a day. Thus on any one day the animal will be trained to a criterion and will learn the response that is correct on that day. After a series of reversals the animal will have learnt and re-learnt both options several times. If proactive interference occurs, animals will find it increasingly hard to remember, on a new day, which option was rewarded last. Their retention of the previously correct option will deteriorate as a function of the number of reversals they have had. Thus animals on late reversals will begin the day without a strong preference to respond to the cue that was rewarded on the previous day. They will thus make a lower number of initial errors and will reach criterion more quickly than animals on early reversals which will still be retaining a strong preference for the correct option of the previous day. Proactive interference is certainly very important in some cases of reversal / .....

/ reversal learning. It has been demonstrated that in some cases a decrement in retention accompanies improvement on a reversal task (Gonzalez et al 1967). However, this theory cannot account for improvement in reversal learning in animals trained continuously (not in separate sessions), nor can it account for changes in the rate of error elimination, only for reductions in the initial number of errors. Improvement in reversal learning does occur in animals trained continuously, and improvements in rate of error elimination are common. Although proactive interference can account for some changes it will not serve as a general explanation for all changes in reversal learning.

Another theory has been suggested by Mackintosh (1969) based on attentional mechanisms postulated by Sutherland (1964). This theory assumes that discrimination learning involves two distinct processes; learning to attend to the relevant stimulus dimension, and learning to associate appropriate responses with specific stimulus values on the relevant stimulus dimension. For example, consider a T-maze in which one arm is black and the other white. Animals are rewarded for turning into the black arm of the maze irrespective of its position. Sutherland's theory suggests that the animal must learn two seperate things; to attend to the relevant stimulus dimension of brightness and ignore other parameters such as position; and to learn to make appropriate responses to specific values of this parameter, i.e. to enter the black rather than the white arm of the maze to obtain reward.

Now / .....

/ Now consider what happens when this discrimination is serially reversed. If animals continue to attend to the brightness parameter they may re-learn the discrimination more quickly becuase they will only have to learn to attach new responses to the stimulus values and not have to re-learn which parameter is correct, i.e. they will not have to re-learn that brightness must be attended to and not position or any other parameter. If they fail to continue to attend to the brightness parameter they will have to re-learn both which parameter is correct and what responses to give to each value of it. They may begin by responding to an irrelevant parameter such as position. Mackintosh suggests that differences in the ability of animals to maintain attention to the relevant parameter after reversal may explain differences in ability to improve over a series of reversals. This theory will also account for the behaviour of animals in probability learning situations. "In both serial reversal and probability learning situations a single cue remains relevant throughout the experiment: the occurrence of reward is predictable on the basis of this stimulus dimension and no other. Both situations, however, involve inconsistent reinforcement of the two values of the relevant dimension; and successful performance on either depends upon the maintenance of attention to this relevant dimension in spite of this inconsistency of reinforcement. The simplest explanation, therefore, of the behavioural differences between rat, bird and fish, is to suggest that the three classes of animal differ in the extent to which they can learn to attend to a given cue when it is not consistently correlated with reinforcement (Mackintosh 1969)."

There / .....

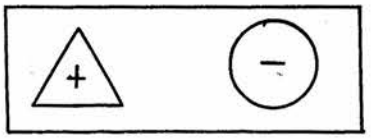
/ There is good evidence that attentional mechanisms play an important part in discrimination learning but as Mackintosh says "at present it is not possible to translate the vague hypothesis that serial reversal improvement is partly due to the development and maintenance of attention, into a formal analysis of serial reversal performance" (Mackintosh 1969, p159). Attempts to formalise this theory have not proved very successful (Warren and McGonigle 1969). Certainly this theory will not account for the behaviour of all animals on reversal tasks.

Chimpanzees (Schusterman 1962) and rhesus monkeys (Warren 1966) acquire a 'win-stay, lose-shift' strategy during reversal learning. That is to say they continue to respond to one of the alternatives until they fail to obtain reward and then immediately switch to the other. Cats, however, cannot develop such a strategy and it is likely that this form of behaviour is seen only among the primates. Among all animals both proactive inhibition and attentional mechanisms may play a part but, as yet, the precise mechanisms involved remain poorly understood.

Although probability and reversal learning have been studied in a more diverse range of species than any other complex learning problem, several other tasks have been studied in a variety of species. One set of comparative data has been collated by Harlow (1958). He cites data on a series of tests which he has classified according to the 'degree of ambiguity' which they contain. Degree of ambiguity is intended as a measure of the complexity of the factors which / .....

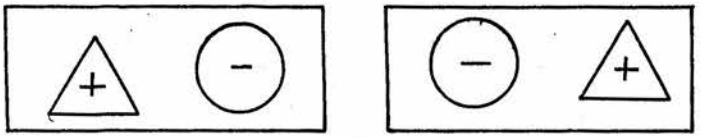
/ which interfere with successful problem solving. The simplest kind of discrimination problem on Harlow's scheme contains no ambiguity; such as the positional discrimination shown below. The shape on the left is rewarded and the one on the right is not. Positional information as well as any other cues remain constant from trial to trial.

Representative positional discrimination



A first degree of ambiguity is introduced by making position irrelevant, as below, so that in different trials the correct stimulus will occupy different positions.

Representative object discrimination



trial A trial B

Both of these elementary problems have been shown to be solvable by a diverse set of species ranging from nereid worms to elephants and rhinoceroses. Although the particular cues to be discriminated vary from species to species and despite gross differences in sensory and motor capacity all the animals take a roughly equivalent number of trials. Thus, on these simple discriminations no meaningful phyletic trends are suggested on the basis of error scores. Of course, if we were to look at many scores of behaviour and tried to find out what, in total, the animals had learnt about the situation, / .....

/ situation, then differences would show up. Unfortunately, most psychologists tend to measure errors only. This perhaps leads to an underestimate of the diversity of behaviour found among different species.

A second degree of ambiguity is added by making the object ambiguous as well as the figure, as shown below. This is the so-called oddity problem.

Representative oddity problem

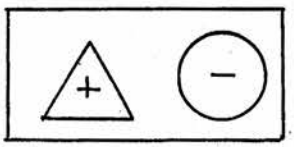
trial A trial B

The figure which is the odd-one-out is rewarded regardless of its position or its shape. This added ambiguity makes this problem impossible for all except the higher mammals. Primates are able to learn this discrimination relatively easily. One cat has been known to solve it (Warren 1960) and pigeons (Ginsburg 1957) and rats (Wodinsky and Bitterman 1953) can solve simplified versions of the problem with difficulty.

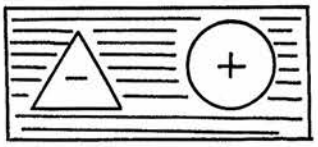
Another degree of ambiguity may be added by making the whole configuration of odd/non-odd ambiguous. This can be done by making some property of the background decide whether odd or non-odd figures are to be rewarded on any particular trial. Many human beings are unable to solve this problem, although monkeys and apes have been known to solve it without difficulty. One chimpanzee has solved a problem containing five such degrees of ambiguity (Nissen 1951).

Another / .....

/ Another one-degree ambiguity problem is shown below. Again both position and object are ambiguous. In this example the colour of the background decides which of the two shapes is rewarded on any particular trial.



trial A



trial B

Rhesus monkeys (Warren 1960a) and cats (Warren 1960b) were compared in this situation. The monkeys learnt to use the background cue while the cats, although being affected by this cue, did not learn to use it as a signal indicating which shape was correct.

In this problem, as well as in several of the others already discussed, an element of 'conditionality' has been introduced into the situation; one stimulus modifies the value of another. Some experiments recently performed in Russia are of a similar type. In these problems one stimulus, A, is rewarded and another, B, is not. However, stimulus A ceases to be rewarded if stimulus C is present. Similarly, B is rewarded when C is present. Stimulus C reverses the values of the other two stimuli. Only chimpanzees, baboons and dogs could learn to adjust their responses appropriately (Voronin 1962).

A similar problem has been tried with rhesus macaques and cats (Warren 1965). Four objects were presented in pairs, each object was positive in one context and negative in another, so that accurate performance depended on varying responses to each object in terms of the other discriminandum presented on any particular trial. Both species were able

to / .....

/ to solve this problem, Rhesus monkeys could even form a conditional discrimination learning set and transfer to other conditional discriminations with different cues.

In a final problem of this type, baboons and dogs were shown to be able to respond to a reinforced combination of light and sound stimuli, and not to respond to either light or sound alone. Fish failed completely to discriminate between the compound stimulus and its components presented separately. Rabbits failed to discriminate as well as dogs but performed more accurately than the fish (Voronin 1962).

Further comparative data comes from work on the formation of learning sets. Learning set formation refers to progressive improvement in learning consecutive discrimination problems. One form of set learning, increased efficiency in learning repeated reversals of the same discrimination problem, has previously been discussed.

The formation of learning sets has been demonstrated in rats, squirrels, cats, raccoons, weasels, skunks, ferrets, pigeons, marmosets and a whole range of monkeys. (Warren 1965). There seems to be systematic trends in the speed with which learning sets are acquired in the different animals. A rat has to be presented with some 800 problems before it begins to learn the 'principle' behind the problem and starts to score above chance on new problems. Squirrels perform about as well as rats but learn more slowly and attain a lower asymptotic level of performance than cats, raccoons or pigeons. All of the non-primates perform less well than marmosets, and there is a steady improvement through a series / .....

/ series of monkeys from marmoset, squirrel monkey, cebus monkey, spider monkey to rhesus macaques. Rhesus macaques show improvement after the first few problems and may reach a perfect performance in four or five hundred problems.

In conclusion, studies on the comparative psychology of learning have shown that, although little difference is seen in error scores between animals on simple discriminations, on more complex conditioning and discrimination tasks there is an orderly improvement in the efficiency of learning within the vertebrate series. As yet few invertebrates have been tested in this way, but the data on the Octopus shows that it performs more efficiently on multi-reversal tasks than the fish that have been tested.

It is difficult to isolate the factors which make one task harder than another, or which make a species arrive at one solution rather than another. Harlow points out that in many cases the animal is having to learn not to respond to inappropriate features of the situation. Although it is doubtful whether "all learning and all thinking may be regarded as resulting from a single fundamental operation, the inhibition of response tendencies " (Harlow 1958), clearly learning to treat certain cues as relevant and others as irrelevant is very important in complex discrimination learning. However, attempts to develop ideas concerning 'relevant' and 'irrelevant' cues into a comprehensive attentional theory of discrimination learning (Sutherland 1964) have not proved highly successful (Warren and McGonigle 1969). / .....

/ 1969). Even in probability and reversal learning situations several different effects must be taken into account. In conditional discriminations, oddity problems and set learning the underlying processes are scarcely understood at all. In conditional discriminations it is necessary for the animal to be able to take the context of any cue into account as these tasks involve cues which are reinforced under some conditions but not under others. In the set learning problems it is necessary to transfer information from previous solutions of related problems. This 'learning how to learn' involves responding to the similarities between different problems. Like processes take place in concept formation where animals learn to group different stimuli into classes on the basis of some similarities. Given the present state of knowledge we can only bear in mind the main factors which seem to be important in these learning tasks.

So far, most of the experiments discussed in this introduction have concerned learning in vertebrates. This reflects trends in research, the great majority of learning studies have been concerned with vertebrates, particularly the rat. However, a number of interesting phenomena have been discovered in experiments with invertebrates. The simplest animals that clearly exhibit trial and error learning appear to be the planarians. In one study planarians were presented with a choice of two chambers, one dimly lit and one brightly lit. If the brightly lit chamber was chosen, the animal was rewarded by having the apparatus filled with water; if the dimly lit chamber was chosen there was no reward. The planarians were able to learn to choose the brightly / .....

/ brightly lit one. In order to test for the effects of an unlearned preference for the bright chamber, the experiment was repeated, except that the dim chamber brought water. In this case, the dim chamber was chosen, suggesting that true trial and error learning had occurred, (Best and Rubinstein 1962).

Recent research on nereid polychaetes and molluscs has enabled speculation about the possible evolution of associative learning. A series of experiments on Nereids (Evans 1966a,b,c) showed that in certain situations adaptive modifications in behaviour can occur as a result of experience. However, these changes do not appear to be manifestations of associative learning. Nereids can be kept in glass 'burrows' in the laboratory and will show quite normal tubiculous behaviour. If punished with electric shock they withdraw and if presented with food they crawl out to the ends of their tubes. When shock is paired with light the animals withdraw more often to the light alone after training. Similarly, if food and light are paired the worms show a greater frequency of approach to light alone than previously. This gives an impression of associative learning but, in fact, the temporal continuity of the two stimuli is unimportant. The same changes in behaviour are shown when food or shock are presented between trials instead of being paired with the light stimulus. It appears that reward or punishment 'sensitises' the animal to respond in a particular way to other stimuli.

The / .....

/ This sensitisation effect can be seen in another situation. Nereids can learn to avoid an electric shock at the end of a perspex channel, either by reversing in the channel or by remaining stationary in it. The performance of worms punished outside the apparatus is found to be indistinguishable from that of worms punished at the exit of the channel. The animal has not learnt to associate the exit with shock. Rather, the punishment has sensitised the reversal response which is a normal part of the worms' behaviour.

Experiments on the pulmonate snail Physa suggest that this animal also can be sensitised but not conditioned, (Wells 1971). The snail retracts its tentacles and pulls down its shell over its head in response to electric shock. Apparent conditioning is produced when light and mechanical shock are paired with electric shock. Identical results are obtained, however, if a series of shocks is given alone or when electric shocks are alternated with other stimuli.

These behavioural modifications, although non-associative, are still adaptive for the animal. Both Nereis and Physa lack sense organs which can make fine visual discriminations. Although a Nereis eye can detect shadows it has not the capacity to discriminate predators from prey on visual information alone. Given that the animal cannot know exactly what a particular stimulus might mean, it is clearly adaptive to respond in the light of recent / .....

/ recent past experience. If experience has shown that the environment is for the time being hostile (electric shocks in the experiment) then it will be safest to with draw into burrow or shell when a stimulus occurs. However, if recent experience has shown that there is food around then it is advantageous to show exploratory approach to stimuli. The animal thus takes advantage of the fact that favourable and unfavourable events rarely occur at random. Food and predators are likely to arrive and be present for some time. Combined with a tendency to habituate, sensitisation will ensure a level of response appropriate to the state of the world around the animal.

Wells (1968) has suggested that associative learning machinery may have evolved from simpler mechanisms capable only of sensitisation. Only as different inputs became more precisely defined would associative conditioning become advantageous. He suggests an intermediate stage in which some discrimination was possible by the animal being more readily sensitisable to some stimuli than others. Thus different levels of response, although of the same qualitative type, could be given to different stimuli. Quite different responses to different stimuli could emerge as receptors improved and synaptic lability evolved. As Wells (1971) points out, sensitisation or similar processes seem to be present as a component of the adaptive changes of animals even as high up the phylogenetic scale as mammals and octopuses. Octopus can be trained to discriminate / .....

/ discriminate a crab presented alone from a crab presented with a white card behind it. The animal is punished if it attacks this second object. During training the animal often passes through a stage in which it approaches both of the stimulus objects very warily (Boycott and Young 1955).

Among the invertebrates, insects and particularly the Hymenoptera have attracted more attention than any other group. Many experiments suggest that some insects can display quite remarkable learning capabilities. Perhaps the best examples are seen in the landmark learning of bees and wasps.

Ammophila obtains, on its flights to and from the nest, such an exact knowledge of the environment that it can walk back to the nest with a caterpillar, even when forced to detour or after having been displaced up to 40 metres (Thorpe 1950). Philanthus learns the location of its nest from orientation flights lasting only six seconds (Tinbergen and Kruyt 1938), and bumble bees learn from 9-50 second flights (Free 1955).

However, learning in insects often appears not to be 'general' but related to specific situations and specific phases of life. The animal appears to have specialised its learning capabilities to deal with certain situations; so that it may learn very quickly in a particular situation but fail completely in a related problem which appears no more 'difficult'. Some examples will make this clear.

1. Bees can learn a colour marking of a food dish in the / .....

/ the few seconds in which they arrive and begin to feed. If the colour is changed after this period before the bee flies away it will not learn the new colour marking of the dish, all the learning takes place in a defined period from one second before the commencement of sucking to two seconds after (Opfinger 1949, Menzel 1967).

2. The digger wasp catches prey and takes it provision the cell of its larvae. On the first visit to the cell the wasp determines how much food to bring and this estimate is not subsequently altered. If the nest is artificially filled the wasp continues to bring food regardless, on all provisioning visits except the first the animal shows no appreciation of the contents of its nest. (Baerends 1941).

3. If a food dish is moved while a bee is feeding it will signal the route it flew to it when it returns to the hive although it returned by a different route (Lindauer 1963). In general, bees, wasps and ants have to learn the approach and return journeys to food sources separately (Schneirla 1946, Weiss 1953).

4. Bees learn floral scents quickly when they are associated with food. When other kinds of odour are present instead the bee will learn about them only with the greatest difficulty or not at all. This effect is not due to failure to perceive the scent nor to a repellant effect of the odour (von Frisch 1956, 1967).

Among / .....

/ Among different figures and colours, only those cues which also release spontaneous approach flights will be learnt as food cues by bees, although many other cues can be perceived. It appears that bees, ants and wasps, at least, have evolved highly specific learning capabilities. Obviously, for animals with small brains and short life spans this is of considerable advantage. Learning is essentially a process enabling adaptation to changing situations; for every species certain types of situation are going to be met with very commonly and it will pay to be prepared to deal with these situations. The idea of 'intelligence' implies a general learning ability. Clearly, we must be very careful in applying this concept to animals like insects which appear 'pre-programmed' to deal with certain situations.

Vertebrates too are adapted to learn about certain things in certain situations. Garcia and Koelling (1966) gave rats "bright-noisy, saccharin-tasting water". That is, they allowed rats to drink saccharin flavoured water whilst a bright light was turned on and a noise sounded. At the same time as they drank they were X-irradiated, a treatment which the animal cannot detect but which makes them feel ill several hours later. The rats acquired a strong aversion to the taste of the saccharin but not the light or noise. Only one trial is necessary for them to associate taste with illness even though the onset of illness occurs several hours after the experience. If the same experiment is carried out but the rats are given electric shock instead of X-irradiation they / .....

/ they become averse to the bright-noise but not to the taste. In each case the 'logical' association is made. Thus, here is a situation in a mammal where certain associations are very easy to form and other 'illogical' assumptions are difficult to condition.

Even man is born with a propensity to learn certain things. It now seems very likely that some of the essential properties of language; the ability to generate an almost infinite set of sentences after hearing only a small selection, and the similarities of structure of 'baby talk' in different languages, make it necessary to postulate an 'innate pre-structuring' of our language capability (Chomsky 1969). Many other examples of a propensity to learn certain things can be given (Seligman 1970). Cats find it easy to learn to escape from a puzzle box by pulling a string or pushing a button, but it is very difficult for them to learn to lick or scratch themselves to make the door open. The cat makes use of these responses to clean itself and it is 'illogical' for them to be of any value in escape behaviour. Similarly rats easily learn to jump or run to avoid shock but find it very difficult to learn to press a bar to avoid shock. In general, items from the natural defensive or escape repertoire of animals can most easily be used in avoidance and escape conditioning. Conversely, natural food-getting responses can very easily be used in experiments with food reward. Pigeons extremely readily learn to peck lighted keys to obtain grain although it is almost impossible to make pigeons use this response to avoid shock.

Although / .....

Although vertebrates are clearly prepared to associate certain things, studies on the comparative psychology of learning described at the beginning of this thesis suggest that general trends in problem solving ability can be detected. Whether these tests can be applied meaningfully to insects remains to be seen. Insects, because of their small brain size and short life span, may be 'prepared' to a high degree to learn about certain things in certain situations but may have little or no general ability or 'intelligence'.

The main points of this introduction may be summarised as follows. Comparative studies of the behaviour of animals on probability and reversal learning tasks have revealed a systematic pattern of variation. In general, the 'higher' the animal the more efficient is its behaviour in these situations. These comparative studies have also helped throw light on the mechanisms underlying these changes in behaviour. Several theories concerning these mechanisms have been discussed; it is likely that each offers a partial explanation of the phenomena although none of them nor any combination of them as yet can produce a complete explanation. Comparative studies on tasks other than reversal and probability learning; studies of conditional problems, ambiguity problems and set learning support the view that there is an orderly progression of increased learning capacity as one ascends the phylogenetic scale. Nearly all these studies stem from work on vertebrates. At a much lower level research on polychaete worms and molluscs makes it possible to speculate about the possible evolution of associative learning. Insect studies suggest / .....

/ suggest that these animals are specialised to learn about specific things in specific contexts. However, most insect research has been carried out by ethologists and this conclusion may be more a result of the kinds of situations studied by ethologists than of the animal itself. Vertebrates also are 'prepared' to associate specific things of relevance to their natural life. However, whereas vertebrates or at least mammals appear to have some 'general' problem solving capability, insects may possess only a set of specific 'programmes'.

There may thus be said to be three main themes in this thesis; comparative aspects of learning ability, attempts to explain these abilities in terms of underlying mechanisms and the significance of specific 'prepared' abilities as against a general 'intelligence'.

The experiments to be described study learning in two species of insect in relation to these points. The two species chosen were the cockroach Nauphoeta cinerea and the honey-bee Apis mellifica. These two species were chosen because they were thought likely to be very different on the parameters under investigation. The cockroach appears to lead a life in which learning plays little part and previous descriptions of its learning capability suggest 'that it is limited to the learning of very simple mazes and seldom attains a stage of very consistent performance' (Schneirla 1953). The life of the honey bee involves almost continuous learning and although little research has been carried out on the learning process itself it appears to / .....

/ to have remarkable capabilities. In particular, recent research has suggested that the honey bee has an amazing ability to learn visual concepts (Mazochin-Porshnyakov 1969) and this might be related to its natural flower foraging habits.

After preliminary work in which suitable experimental methods were devised the behaviour of the two species on reversal learning and other 'vertebrate type' learning tasks was examined and related to the pattern of differences between species discussed in this introduction, to current ideas about discrimination learning and to specific abilities related to the natural life of the animal. Some experiments were carried out with the cockroach in a 'natural' situation to assess the relevance of the abilities found in the laboratory. The ability of the bee to form visual concepts was extensively investigated as this appeared to be an example of a highly specific capability adapted to its particular mode of life.

COCKROACH INTRODUCTION.

Cockroaches have been the subject of numerous learning experiments. Szymanksi (1912) first demonstrated conditioning in Blatta orientalis, in a passive avoidance situation. Cockroaches are photonegative and when placed in a box which is half dark and half brightly illuminated they come to rest in the dark side. Szymanski conditioned the cockroaches by giving them an electric shock every time they attempted to pass from the brightly illuminated side to the darkened portion of the box. Eventually they learned to remain in the light side of the box, frequently passing through a stage in which they approached the dark/light barrier but backed away before being shocked.

This situation was also investigated by Turner (1912) with the same species of cockroach. He showed that cockroaches learned to remain in the illuminated side of the apparatus but found that when the light/dark boundary was moved the cockroaches went on avoiding the place where the boundary had previously been. It appeared that the cockroaches had not truly learnt to avoid the dark but rather were avoiding a particular area within the apparatus where they had received shock. Turner suggested that the animals had learnt to avoid this area on the basis of tactile cues. This situation has not been subsequently investigated so it is not known precisely what the cockroach learns in this situation.

The behaviour of cockroaches in multiple mazes has attracted / .....

/ attracted a great deal of attention. Numerous workers have shown that cockroaches can learn a route through an illuminated maze to reach a dark place (Turner 1913, Eldering 1919, Brecher 1929, Gates and Allee 1933, Chauvin 1947, Hullo 1948, Goustard 1948, Viatte 1950, Le Bigot 1952, Verron 1953, Longo 1963, Burleigh 1970). This behaviour does not appear to be explicable on the basis of odour trails. Turner found that cleaning the maze had no effect on errors and Eldering found that changing replaceable paper partitions in her maze had no effect on errors. A thorough investigation with Periplaneta americana (Burleigh 1970) showed that trail substances did not play a part in finding a route through a maze. A large number of animals were run through a T maze in which access to one arm was blocked off. Naive animals were then allowed to run the maze with both arms open but showed no preference for the arm into which the previous group had entered. Caution is needed because it has been shown that in earthworms punishment causes release of an alarm substance which is subsequently avoided (Ressler 1968). Burleigh showed that electric shocks administered to Periplaneta in one arm of a T-maze had no biassing effect on later runs by naive animals. Thus it seems likely that the experiments reported on maze running are due to true learning effects rather than to the presence of odour trails. However, there are very many different species of cockroach and the possibility of odour trails cannot be discounted in the many species that have not been investigated.

Certainly some cockroaches are sensitive to odour.

In / .....

In a Y-tube olfactometer Blattella germanica (Le comte 1948) always choose the arm which has previously been occupied by a cockroach. This odour is water soluble, if the olfactometer is washed with water the animals choose each arm equally often.

Several factors have been investigated in relation to maze learning. A number of workers have studied the effects of removing different sense organs (Turner 1913, Brecher 1929, Chauvin 1947, Hullo 1948, Goustard 1948, Burleigh 1970) in order to understand the overall balance of different sensory factors involved in learning. Nearly all the experimenters claim to demonstrate the overwhelming importance of the antennae. Hullo showed that waxing the antennae in one position almost completely inhibited learning while Turner, Brecher and Chauvin showed that removal of the antennae completely disrupted maze learning. In the same situation both Chauvin and Brecher showed that painting over the eyes had no effect on maze running. However, these results are hardly surprising when it is realised that these experiments were conducted under conditions of uniform lighting and the only available cues were tactile/antennal ones. When the lighting of the maze is assymetrical cockroaches can use the lights as cues to help find the correct arm and under these conditions painting over the eyes or rotating the maze disrupts the learnt pattern of behaviour (Goustard 1948, Burleigh 1970).

These experiments contribute very little to understanding the ability of the cockroach to respond to different cues. Instead / .....

/ Instead of cutting off various sense organs it might have been better to make correct turns contingent upon particular cues. One experiment of this kind stems from the early work of Eldering (1919). She showed that cockroaches could be trained to turn left or right in a simple maze to avoid electric shock. They could also be trained to discriminate between more brightly and less brightly lit alleys with the position of each being randomly alternated, although this took considerably longer than the previous positional discrimination.

A factor which must be borne in mind when designing cockroach mazes is alley width. Viatte (1950) showed that alley width had a powerful effect on rate of learning. Cockroaches showed much faster acquisition in a maze with alley width of 1.25 cms than one of 2.5 cms which was again better than one of 5 cms. However, Burleigh (1970) could find no difference between groups of Periplaneta americana trained in mazes with alley widths of 4 and 8 cms. This factor of alley width may well be related to the distance the antennae of the cockroach reach either side of its body. If it cannot reach both walls of the maze simultaneously, it tends to follow one of the walls, this predetermines which way it will turn at the choice point.

Attempts have also been made to relate the rate of learning to some measure of the complexity of the maze. Chauvin (1947) claimed that in multiple unit T-mazes the rate of learning is a cubic function of the number of T-units comprising the maze. However, further research by Burleith (1970) showed that as well as the number of T-units the configuration / .....

/ configuration is very important. In particular, cockroaches find it much harder to master a maze if they have to make turns in opposite directions at consecutive choice points. Although clearly demonstrating that cockroaches are capable of trial and error learning the studies I have described contribute little towards answering the kinds of questions laid out in the general introduction to this thesis. Even the quite considerable body of work on factors influencing maze learning suggest little about what the animal is learning about the situation or how it solves the maze in relation to other animals. Burleigh's work suggests that the cockroach is influenced strongly by the pattern of the maze and tends to behave according to a relatively simple programme in that a turn to the correct side at the first choice point influences the cockroach to turn to the same side at the next junction. However, we have little knowledge of the stimuli which the animal is capable of abstracting or of complexity of problems that it can solve. This makes comparison with other species almost impossible.

Lawson (1965) pointed out that although a maze problem may be suitable for ants which live in underground galleries it was not the kind of situation met in the life of the cockroach and would not necessaruly allow the animal to demonstrate its full learning potential. However, his own experimental situation, designed to overcome this problem, seems even less well suited to the animal. He examined the behaviour of Periplaneta americana when placed on a wooden island standing in water and noted the time taken to escape, a feat often achieved by leaping and then swimming. Animals did / .....

/ did escape more rapidly with experience of the situation but it was unclear what they were learning.

A much better example of what can be done is provided by a study performed by Schneirla (1953) on the ant Formica. In his experiment ants and white rats were both tested in a maze containing six blind alleys. The learning curve of errors against trials was similar in form in both species although ants needed more runs to master the situation. However, "the rats learnt the pattern in a facile manner with choice point adjustments beginning from the first run, with a minimal repetition of errors, and without any identifiable signs of distinctive stages. In contrast the progress of the ants was laboured, with a definite tendency to repeat certain errors; also with distinct stages of generalised and segmental learning in that order, pre-requisite to eventual mastery of the situation". After the animals had learnt the maze they were made to re-run it in reverse. The ant was unable to transfer its previous experience and treated it as a completely new problem while the rats very quickly learnt to run the reversed maze. This supports the view that the ant learns a highly specific and stereo-typed sequence of acts while the rat learns something more general. This study is interesting in that instead of just measuring error scores (which were of the same form in both animals), some attempt was made to compare behaviours of the animals and to find out what they had learnt about the situation.

In many of the experiments to be described in this thesis a / .....

/ a similar attempt is made to study and compare many scores of behaviour in a learning situation.

EXPERIMENTS WITH THE COCKROACH

NAUPHOETA CINEREA. (Oliv).

3.

MATERIALS AND GENERAL METHODS.

The cockroaches used in the series of experiments reported in this thesis were of the species Nauphoeta cinerea (Olivier). In general, this species has not been widely studied but it has been the subject of a number of experiments performed in Edinburgh on territoriality and aggression (Ewing 1967, 1970, 1972; Manning & Johnstone 1970) and on activity (Cafferty 1969; Reynierse et al 1972). The animals were kept in either a set of large culture tanks or in a small culture tank.

The large culture tanks were 60 cm x 30 cm x 30 cm and contained around a thousand animals each. The cockroaches were fed on a diet of rat cake, apples and water. Cardboard egg boxes were placed in the tanks for the animals to hide under. For experimental purposes only adult male animals were used. They were collected from the tanks while still in the teneral stage, i.e. while still newly moulted into adults. After collection the animals were isolated in glass crystallising dishes 8 cm in diameter and 5 cm high. They were always kept isolated for at least a week before experiments began. The crystallising dishes contained a piece of rat cake and small vial of water with a ball of wet cotton wool pushed into the open end.

The small culture tank was a circular glass tank 25 cms in diameter and 8 cms high. It usually contained about forty adult animals, all derived from a single pair of cockroaches. The tank contained rat cake, a dish of water soaked cotton wool and several sheets of paper for shelter.

Adult / .....

Adult male animals were marked about once a week with a colour-coded spot of paint. Each animal was marked on its pronotum. When animals were required for an experiment they were selected to be of approximately the same age (the same colour mark) and individually marked with a set of paint spots. Each cockroach was removed from this tank when required for an experimental session and replaced immediately after. They thus spent all their time in the culture tank except for brief experimental periods.

All the animals were kept and experimented upon in a light and temperature controlled room. The temperature was kept at 77°F, and the lighting on a schedule of twelve hours dark, twelve hours light. During the light phase of the cycle the room was illuminated by neon strip lights, all lights were switched off in the dark phase. The experiments were carried out in the dark part of the cycle. When an experiment was in progress all the culture tanks were covered with a black cloth to prevent them being influenced by experimental lighting conditions.

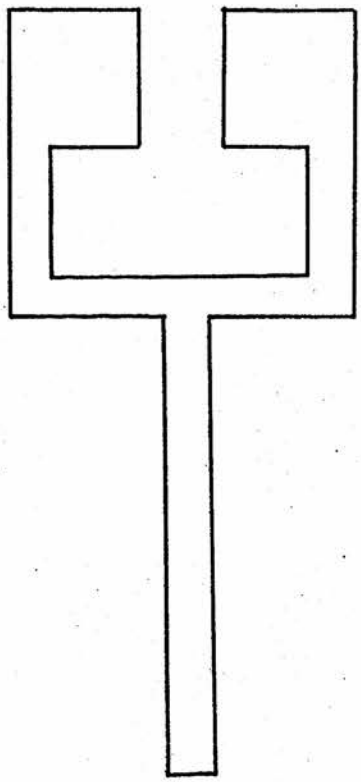
4.

EXPERIMENTS WITH DARK REWARD.

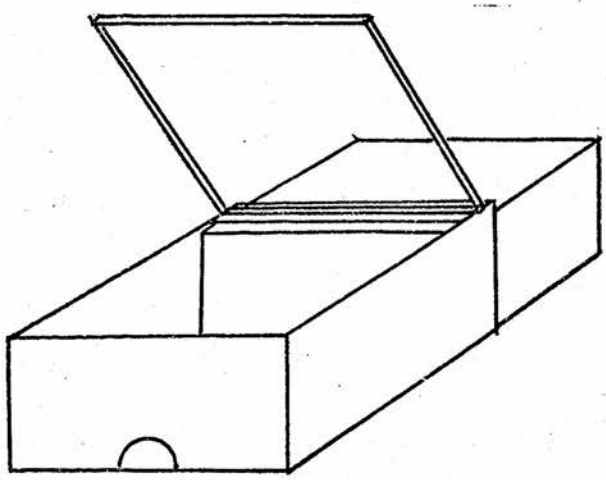
FIGURE ONE.

PLAN of T-MAZE

1/3 actual size



COCKROACH INTRODUCER



Introduction

The cockroach Nauphoete cinerea is not a common laboratory animal and has been the subject of only one learning study. The first problem to be faced with such a little known animal is that of finding experimental conditions under which learning can be demonstrated. Suitable reinforcers must be found and apparatus designed to fit the cockroaches perceptual and motor systems. In many experiments with cockroaches it has been found that the animals will readily learn to run simple mazes in order to escape from bright light. This kind of situation was investigated first. In the experiments described below cockroaches were required to learn a correct turn in a brightly lit T-maze to find their way to a dark place.

Materials

The maze used was a simple T of the floor plan shown in figure one. The walls of the maze were constructed from a set of wooden blocks a quarter of an inch high. The maze was assembled by placing the blocks around a floor plan template. As the blocks were interchangeable any part of the maze wall could be swapped with any other part. This was a great help in controlling for odour trails. Also each block was coated with polyurethane varnish so that it was washable.

The maze was laid out on a black 'Formica' table which served / .....

served as the maze floor. A glass plate was placed over the top of the maze and marked out in one inch squares.

A special box was used to introduce cockroaches into the maze and is shown in figure one. Cockroaches were placed in this box and the perspex lid closed. A small hole which led into the maze was the only exit for the animal. If the cockroach was reluctant to move out into the maze the back wall of the box could be slid forward and the animal given a gentle push in the direction of the exit hole. This apparatus was designed to reduce handling of the animal to a minimum. Cockroaches become very agitated if handled for longer than a brief period, they may even become so stressed that they will die two or three days later. Using this apparatus it was possible to tip the cockroach straight from its home vial into the box and then into the maze without handling it.

The apparatus was illuminated by a sixty-watt bulb placed fifteen inches above the choice point. A dark place was provided at the end of one of the arms by blacking out the area with a piece of cardboard. As the end arms of the T-maze have a bend in them it is not possible for the cockroach to see the dark place from the choice point.

Subjects

The experimental subjects were ten adult male Nauphoeta cinerea. They were collected from a large culture tank shortly after their final moult and kept individually in glass / .....

/ glass crystallising dishes for a week prior to the beginning of the experiment. Each dish contained a piece of rat cake and a vial of water stoppered with cotton wool.

Methods

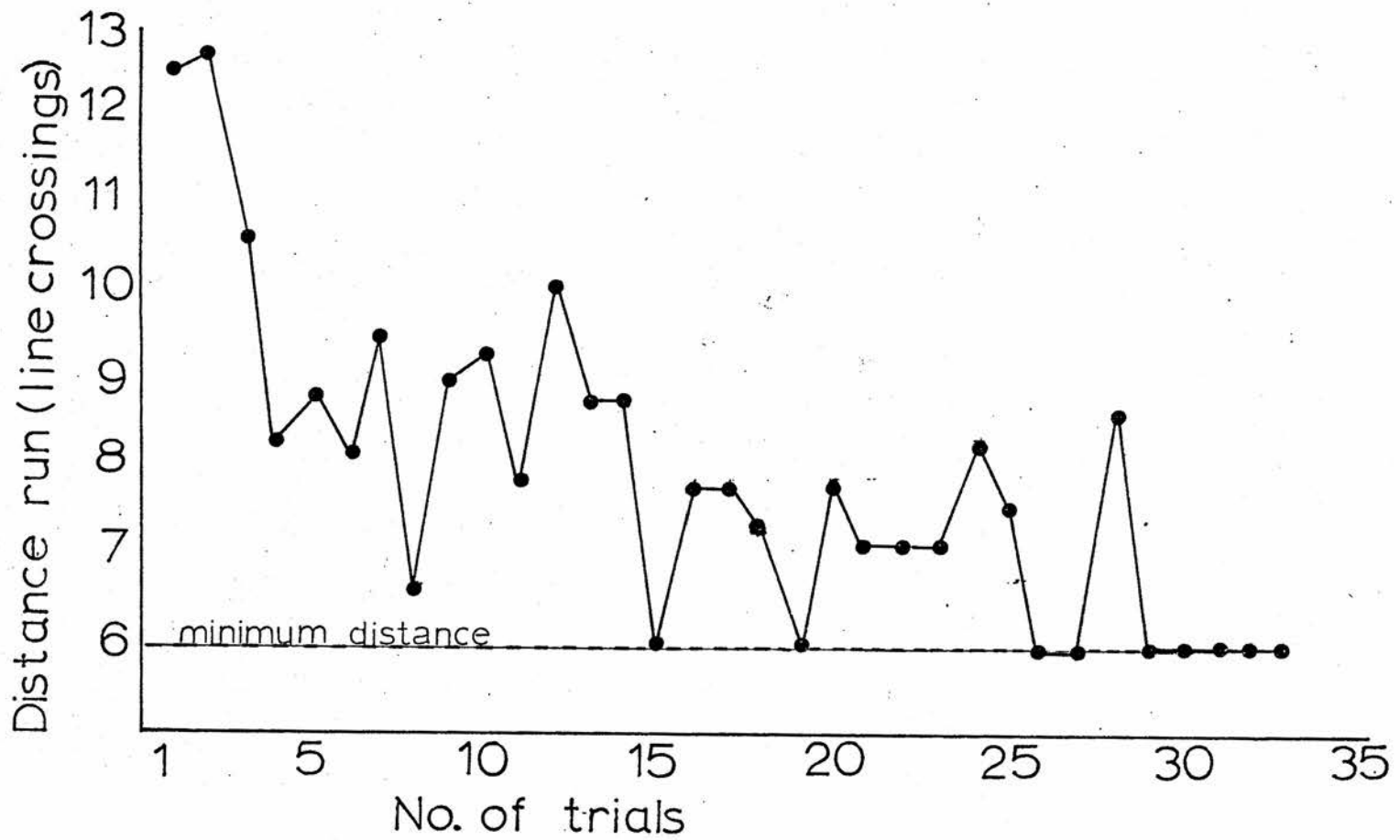
Each animal was trained on a simple positional discrimination For five of the animals the dark place was at the end of the left hand arm of the T-maze and for the other five the right. Each animal was placed in the introducing box and persuaded to enter the maze. If it made a correct turn it was allowed to remain in the dark area for five minutes and was then transferred to a small black perspex dish while the apparatus was cleaned. If the animal made an error it was allowed to correct it, i.e. the animal was left in the maze until it found the dark place. Sometimes a cockroach would stop in the main alley or in the illuminated arm, if it did not move for five minutes it was removed from the maze. The apparatus was then cleaned and another trial initiated.

The total distance travelled by the cockroach before reaching the goal was recorded on each trial. The distance was measured in terms of the number of line crossings made by the animal. As mentioned previously the glass plate covering the maze was marked out in one inch squares. The animal was considered to have crossed a line every time its body passed completely from one square to another. The minimum distance the cockroach could travel to reach the dark place was six line crossings. Training continued until the animal ran the shortest route to the goal in nine out of ten trials.

Between / .....

FIGURE TWO.

Learning curve for cockroaches learning a positional discrimination in a T-maze.



Between trials the floor, glass and blocks were washed with water and then alcohol. The blocks were then randomly re-arranged to form an identical floor plan.

Results

Nine out of the ten animals attained the criterion. Of these nine animals, eight reached the criterion within eighteen to thirty-three trials. The ninth animal frequently came to rest in the region of the choice point and eventually took sixty-three trials to reach criterion. The one animal that did not reach criterion learnt to run to the dark place but always by first making an incorrect turn. Although this meant it passed the choice point twice it never learnt to shorten its route. Another animal was trained to replace this one. The mean number of line crossings made by the group of ten animals which successfully reached criterion is plotted against trials in figure two. Except in the final stages of the graph each point represents the mean of results from all ten animals. After trial eighteen the results are drawn from successively fewer animals as they reach criterion and are withdrawn from the experiment. The curve clearly demonstrates that the animals learn to progressively shorten the distance they run in reaching the dark place.

Conclusions

Although the animals learnt a simple positional discrimination the results are rather disappointing. The cockroaches took a long time to learn the discrimination and there was high individual variability. Individuals did not show consistent changes in behaviour but showed short runs of errorless performance / .....

/ performance followed by errors again. Not infrequently animals would come to rest in the straight alley or in the wrong arm of the T-maze. Again, animals that reached the dark goal would often leave it again after a short while and wander about the illuminated maze. This behaviour seemed to increase as the experiment continued. It seemed likely that the light level was not really high enough to motivate the animals to avoid it. However, when a more intense light was tried it was found that many animals 'froze' as soon as they entered the maze. It has been pointed out before (Chauvin 1947) that efficiency of learning in this kind of situation is very dependent upon light intensity. In the hope of finding more efficient experimental conditions an experiment was designed to find levels of light intensity optimal for producing escape behaviour.

Apparatus

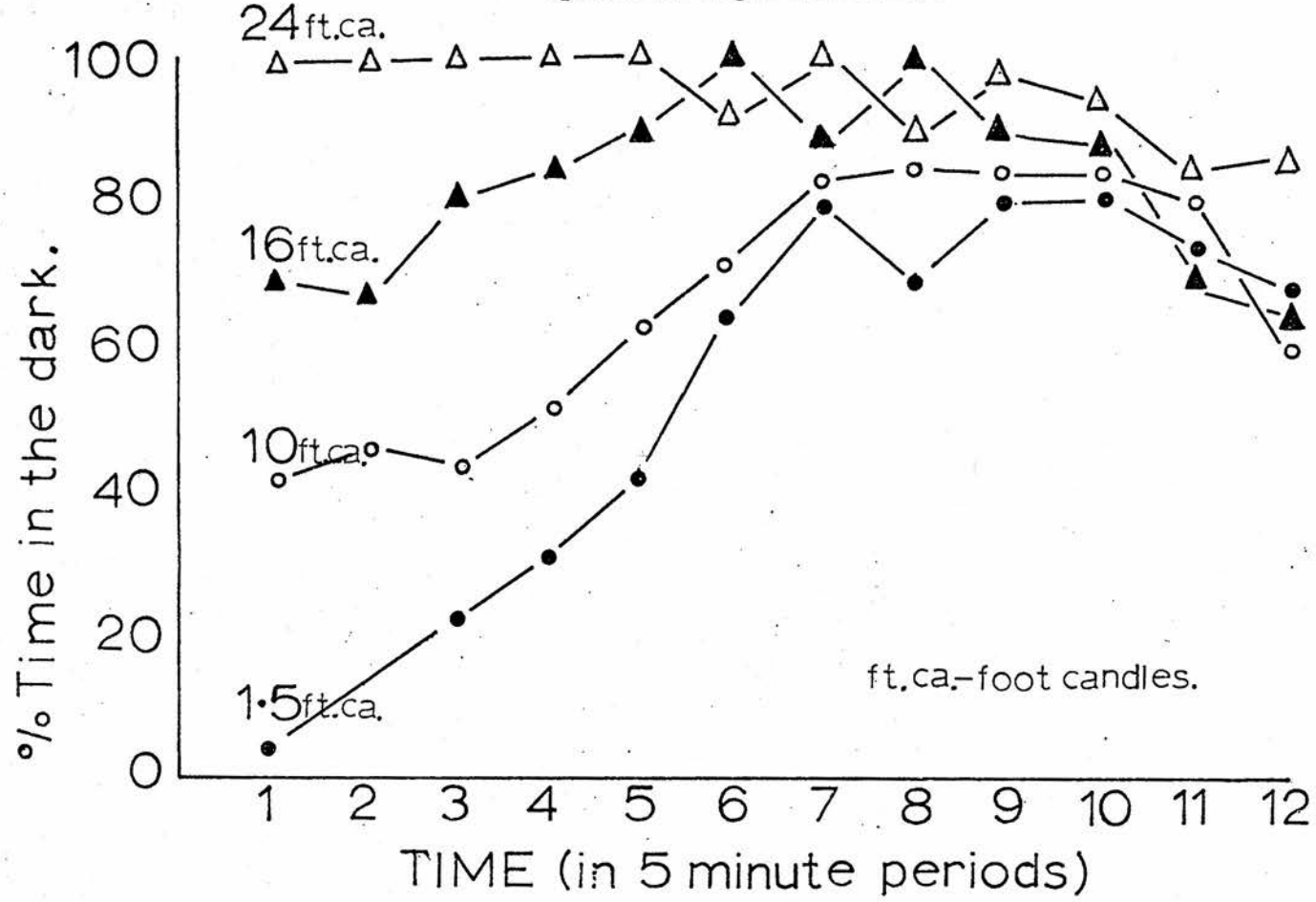
The apparatus consisted of a ten centimetre square arena. The walls and top of the apparatus were made of clear perspex. One half of the arena was blacked out by a thick cardboard sheet placed on top of the apparatus. The other half of the arena was illuminated by a bulb connected to a variable mains resistor. The illumination of this side of the arena could be varied. The light intensity at the arena floor was measured with a Weston Master Universal exposure meter.

Subjects

Thirty adult male Nauphoeta cinerea were used in the experiment. They were collected from a large culture tank shortly after completing their adult moult and isolated in glass / .....

FIGURE FOUR.

Curves showing percentage time spent in the dark by cockroaches over twelve five-minute observation periods. Each curve is for a specified light intensity.



/ glass crystallising dishes for one week prior to the beginning of the experiment.

Method

The light intensity was set at a particular level and a cockroach placed in the lighted half of the arena. The cockroach was allowed to settle down for thirty seconds and then the amount of time the cockroach spent in the dark half of the arena was measured during each of twelve consecutive five-minute observation periods. The cockroach was then removed, the apparatus cleaned and another animal tested. Six light levels were used and five animals were tested under each condition.

Results

In figure four is plotted the percentage time spent in the dark against observation time periods for four of the groups of animals. Each of these groups of animals was tested at a different light intensity, the different groups are shown by separate curves each marked with its associated light level. As each group contained five animals every point on the graph is a mean of five results. It can be seen that a distinctive series of changes in the percentage of time spent in the dark occurs with the time the animals have spent in the apparatus. For clarity, the records for two groups of animals tested at intermediate light levels are omitted from the graph. Their results were consistent with those illustrated and can be consulted in Appendix 1c.

Two main points can be made about the results:

1) / .....

/ 1) The percentage time spent in the dark in the first five minute observation period is closely related to the light intensity. At the highest intensity all the animals spent all the time in the dark while at the lowest level the cockroaches spent nearly all the time in the light. Intermediate intensities showed intermediate values.

2) As time progresses the animals in the lower light levels showed an increasing avoidance of the light. However, after forty-five minutes this tendency appeared to reverse and animals began to spend more time in the light again. To test for the significance of this change the coefficients of quadratic regression were calculated for each of the curves shown. The results from the highest light intensity (24 foot candles) did not significantly differ from a straight line distribution but all the other curves significantly differed from a straight line but not from a quadratic curve. Thus in all except the highest intensity light conditions the curve of percentage time spent in the dark against time shows a rise followed by a fall.

Conclusions

Avoidance of the light in the cockroach is dependent both upon light intensity and the time for which cockroaches have been exposed to light.

These results appear to support the conclusions of Goustard (1958). As a result of a series of experiments with the cockroach Blatella germanica he stated that these animals are not 'photonegative' in any simple sense. Rather he claimed that light has both attraction and avoidance components and the / .....

/ the relative strengths of these components changes with time and with light intensity. These conclusions suggest why the cockroach shows such variable behaviour on a light-avoidance motivated maze problem. Virtually every worker using this technique has drawn attention to the high individual variability in the behaviour of the animals. It seems probable that the tendency to avoid light is changing throughout the experiment. It is possible that this change in behaviour is related to habituation of the compound eye or ocelli or perhaps to a more central change. However, whatever its cause, it is clear that escape from bright light is not a very suitable way of reinforcing the cockroach for running a simple maze. The highest level light intensity group showed consistent light avoidance for the first thirty minutes but it was at this light level that many animals 'froze' immediately they entered the maze. A series of attempts to find a better reinforcer for the cockroach is described in the next three sections.

5.

EXPERIMENTS WITH FOOD REWARD.

Introduction

The previous section showed that it was difficult to produce consistent behaviour in a maze situation when escape from bright light was used as a reinforcer. This technique appeared to be unsatisfactory largely because of the changing aversiveness of light with time. In the experiments described below attempts are made to reinforce solutions of maze problems by access to food. Food reward has been successfully used in learning experiments in many species and it was hoped that it would serve as a reliable reinforcer for the cockroach.

Although some workers (Goustard 1948, Gates & Allee 1933) have mentioned attempts at obtaining food motivated behaviour in the cockroach there has only been one systematic study. Longo (1964) deprived cockroaches (P. americana, Blaberus cranifer) for a week and then gave them rewards of up to twenty-five seconds a day eating. He failed to find any clear evidence of learning in either a T-maze or a straight alley. However, in view of recent studies it is not surprising that the conditions used did not motivate the animal. Cafferty (1969) has shown that cockroaches can survive for remarkably long periods without food. It is not uncommon for cockroaches (N. cinerea) to live for two months under conditions of total food deprivation. After thirty days deprivation only a ten per cent reduction in weight is recorded. Short periods of deprivation / .....

/ deprivation have little effect on the animals interest in food. After five days deprivation no animals commenced eating within half an hour of being presented with food. However, after fifteen days deprivation a cockroach will eat immediately if given food and will continue in bouts for periods of up to two and a half hours. With periods of deprivation greater than fifteen days the amount eaten falls and the latency of eating when presented with food increases once more.

This data suggests that periods of deprivation as short as a week are unlikely to have effects on motivation. My own experiments used deprivation periods of 14, 21 and 35 days.

A problem in the design of the experiment is how to feed the animal a small enough quantity of food so as to sustain motivation over a number of trials. As cockroaches normally eat only twenty milligrammes of food a day (Cafferty 1969) and spend only about five minutes eating it (Ewing 1970) it would be quite easy to satiate an animal on a single trial and then have to spend some weeks waiting for it to be motivated again. This problem was overcome simply by removing the animal after a particular time period had elapsed, although this meant rather frequent handling of the animal.

Apparatus

The apparatus consisted of a T-maze identical with that used in the previous experiment. One of the goal boxes contained the food reward, a piece of rat cake. The apparatus was dimly illuminated by a red ten-watt bulb placed fifteen inches above the choice point.

Subjects /.....

/ Subjects

115 adult male Nauphoeta cinerea were collected from a large culture tank shortly after completing their final moult. They were individually isolated in glass crystallising dishes which contained a cotton-wool stoppered water-vial but no food supply.

Each animal had a small cotton loop stuck onto its thorax with dental wax. The animal could be picked up with forceps by this loop. Handling of the animal in removing it from the maze and transferring to the start could thus be minimised.

Methods

The animals were divided into three groups and were kept without food for 14, 21 and 35 days respectively. Each of these groups was further divided into groups of five animals each with differing conditions of reward time per trial or number of trials per day. The full set of different conditions can be seen in Tables two.

All animals were given a series of one hundred trials in the T-maze. If the animal found the food but did not eat, or if it came to rest somewhere in the maze other than in the goal box it was left for three minutes. If it still showed no sign of eating or moving after this time then it was removed from the maze and the experiment continued. If the animal made an error it was immediately removed from the maze. Between trials the animal was kept in a small plastic dish while the apparatus was cleaned. The intertrial interval was five minutes.

In / .....

In every group, two out of five animals were run with the food reward in one arm of the maze and the other three with the food in the other arm. The animals thus had to learn a simple positional discrimination, either to turn left of right, to reach the food.

Results

The results are shown in table two. The percentage of errors is tabulated averaged for each of the twenty-three groups averaged over blocks of twenty trials. If learning takes place in any group we should expect a reduction in errors with trials. No group shows a consistent trend towards reduction of errors. The figures shown in table two are percentage errors for those animals that did make a choice. Throughout the experiment a great number of animals simply did not complete the run but came to rest in the straight alley of the T-maze. In total, on thirty-two per cent of the trials animals did not make any choice at all and were removed from the maze after the three minute period had elapsed. Also, many animals that did make a correct choice did not eat although they appeared to find the food.

Conclusions

The animals did not learn to make a turn in a T-maze to obtain food, neither did they consistently run the maze or eat when they found food. This was true under a variety of experimental conditions.

A possible explanation for these results is suggested by some recent experiments with Periplaneta americana. These cockroaches / .....

TABLE TWO.

FOOD DEPRIVATION EXPERIMENT.

DEPRIVATION PERIOD OF 14 days.

		PERCENTAGE ERRORS.				
	number of trials/day.	trials 1-20	trials 20-40	trials 40-60	trials 60-80	trials 80-100
¼ minutes reward per trial	2	48	52	46½	45½	53
	5	40	50½	44½	54	48
	10	48½	52½	48	50	56½
1 minutes reward per trial	2	49	46	52	49½	51
	5	53½	49	48	51½	48
	10	45	44	51	52½	49
5 minutes reward per trial	2	45½	50½	50½	48	54
	5	--	--	--	--	--

TABLE TWO continued.

DEPRIVATION PERIOD OF 21 DAYS.

		PERCENTAGE ERRORS.				
	number of trials/day.	trials 1-20	trials 20-40	trials 40-60	trials 60-80	trials 80-100
¼ minutes reward per trial.	2	50	44½	52½	52½	46
	5	53	45½	52	56	52½
	10	42½	50½	54	49	55
1 minutes reward per trial.	2	51	43	53	52	52
	5	48½	46½	45½	48	49½
	10	45½	48½	49	53½	49
5 minutes reward per trial.	2	47½	49	56½	51½	47½
	5	45	46½	59	50	52

TABLE TWO continued.

DEPRIVATION PERIOD OF 35 DAYS

	number of trials/day.	PERCENTAGE ERRORS. trials 1-20	trials 20-40	trials 40-60	trials 60-80	trials 80-100
¼ minutes reward per trial.	2	48	44	51	55	53½
	5	50½	44½	48	52	50
	10	45½	46	54½	59	57
1 minutes reward per trial.	2	46½	53½	48	48½	51½
	5	48½	45½	52	53	50
	10	40½	48	54	48	54
5 minutes reward per trial.	2	50	48½	41	58½	40
	5	42	45½	51½	52½	48½

/ cockroaches were found to have a daily feeding rhythm (Lipton and Sutherland 1970), feeding commencing shortly after dark onset in phase with the period of activity recorded at this time. It is possible that cockroaches 'feel hungry' and seed food only at certain times of day. The effect of deprivation may not be to elicit general food seeking behaviour which overrides the circadian rhythm. The behaviour of lugworms appears controlled by internal pace-makers which set off particular behaviour patterns at particular time intervals (Wells 1950). Although these animals may be a special case as they live in a rather constant environment it is possible that some aspects of cockroach behaviour are governed in a similar way. However, the experiments described in the thesis began immediately after lights off and continued through the 'night'. The same groups of animals were always tested at the same time of day and it seems unlikely that none of the groups would have been tested at a time when the cockroach is normally 'hungry'.

Another possible explanation of the failure to obtain learning is that the negative effects of handling the animal in the goal box counterbalanced the reward value of the food. However, cockroaches did not learn to avoid the area where they were handled any more than they learnt to visit it, rather they showed random choice behaviour. It seems unlikely that the effects of handling would exactly counterbalance the effect of food reward.

It is possible that the motivational system of the cockroach / .....

cockroach is very different from that of mammals. It has been shown that Nauphoeta cinerea does not show an increase in activity as a result of food deprivation (Reynierse, Manning and Cafferty 1972) as do many vertebrates and at least one invertebrate, Drosophila melanogaster (Connolly 1966). Whatever the facts of the cockroaches food regulation system are found to be, access to food is clearly not a useful way of reinforcing the animal in a conventional maze situation.

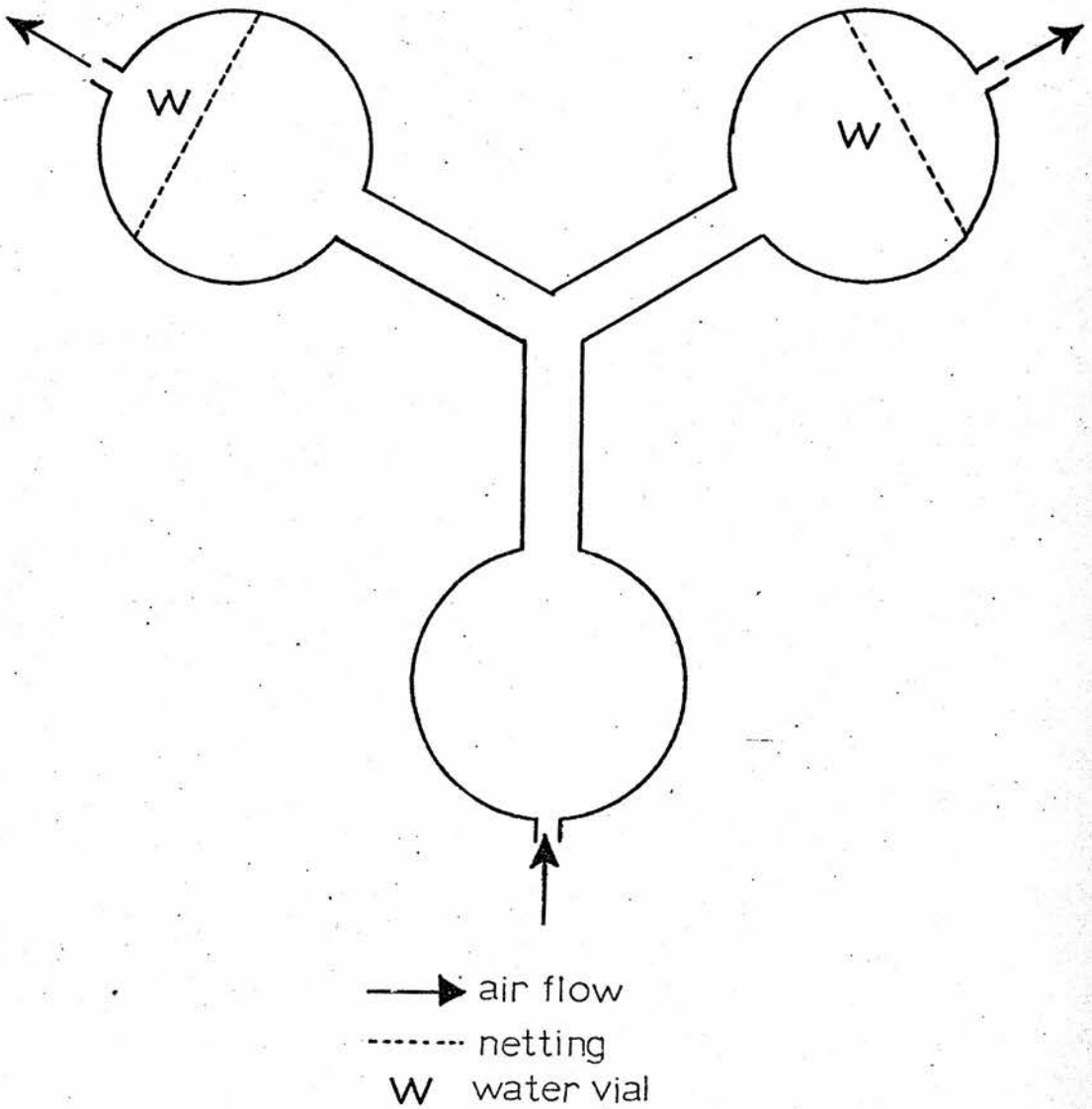
6.

EXPERIMENTS WITH WATER REWARD.

FIGURE FIVE.

PLAN of Y-MAZE

2/3 actual size



Introduction

In this section some experiments are described in which cockroaches are rewarded for a correct turn in a Y-maze by access to water. It has already been shown that neither escape from bright light nor access to food served as satisfactory reinforcers in a similar situation. However, it was thought that water reward may be effective as there is good reason to believe that cockroaches are fairly sensitive to water deprivation. If a large culture tank of cockroaches is left without water for a few days and then a dish of water is introduced into the tank there is immediately a huge rush of animals to the water source. Similarly, it has been shown (Cafferty 1969) that cockoraches will drink immediately they are given an opportunity after only five days deprivation.

The main problem with using water reward is, as the observation above shows, that cockroaches can detect water from a distance. The apparatus used was specially designed to overcome this problem.

Another problem is that cockroaches normally spend only about one minute a day drinking (Ewing 1970). Reward times were designed with this figure in mind.

Apparatus

A Y-maze was used and is shown in figure five. It was built of clear perspex and its walls were one inch high. A vial of water was present in both arms of the maze but in only / .....

/ only one arm could the cockroach reach the water. In the other arm the water supply lay behind a sheet of mosquito netting. By this technique it was hoped to equalise the water vapour cues coming from each arm. To minimuse the presence of water vapour in the maze a steady stream of air was kept flowing from the start box to the goals. An air inlet had been drilled in the start box and in each of the goal boxes. Air entered through the hole in the start box and was drawn from the goal boxes by an electric pump.

The apparatus was dimly illuminated by a red ten-watt bulb placed fifteen inches above the choice point.

Subjects

Sixty male Nauphoeta cinerea were collected from a large culture tank shortly after completing their final moult. They were individually kept in glass crystallising dishes which contained a piece of rat cake but no water supply.

Methods

The animals were divided into three groups and deprived of water for 14, 21 and 28 days respectively. These groups were further divided according to the number of trials a day they were to receive and the number of seconds they were allowed to drink on each trial. The full set of conditions is laid out in table three there being five animals in each of the final twelve groups. In each of these sub-sub-sub-groups two of the five animals were trained to turn one way in the maze and the other three the other way. The animals thus had to solve a simple positional discrimination in order to reach the vial of water.

On / .....

On each trial the air pump was turned on and a cockroach placed in the start box of the maze by means of the cotton loop on its back. A close fitting perspex lid made the apparatus air tight. If the cockroach refused to run the apparatus it was removed after three minutes. If it made an error it was removed immediately but if it made a correct turn it was allowed to drink for the prescribed time before being removed. The intertrial interval was kept constant at five minutes whether or not the animal made a correct choice. All animals were given 100 trials, in groups according to the conditions laid out in table three.

Results

The percentage errors are averaged for each group of five animals over twenty trial periods and shown in table three. It can be seen that none of the groups show a consistent reduction in errors and they never make choices significantly different from chance. On twenty-seven per cent of the trials the animals did not run the maze but came to rest in the approach alley. However, unlike the experiment with food reward, if a cockroach did find the water it virtually always drank.

Conclusions

Under a variety of experimental conditions cockroaches did not learn a positional discrimination in a T-maze to gain access to water. It is difficult to suggest reasons for this failure. It is possible that cockroaches have a pronounced daily rhythm of drinking which did not coincide with my own testing times. However, as in the experiments with food reward testing / .....

TABLE THREE.

WATER DEPRIVATION EXPERIMENT.

			PERCENTAGE ERRORS.				
		number of trials/day.	trials 1-20	trials 20-40	trials 40-60	trials 60-80	trials 80-100
10 seconds reward per trial.	14 days deprived.	2	49	51	48	48	60½
		5	61½	60½	43½	46½	55½
	21 days deprived.	2	60	54	57½	60	48
		5	44	41½	60	48½	50
	28 days deprived.	2	53½	43½	61	49½	52
		5	49	56	55½	44½	40½
40 seconds reward per trial.	14 days deprived.	2	39	41	44½	42	47
		5	41	60	38	63½	48½
	21 days deprived.	2	51	46½	51	44	42½
		5	39	54½	44½	50	40½
	28 days deprived.	2	52½	50½	55½	43	53½
		5	44	50	47½	45½	60½

testing began immediately after 'lights-off' and continued throughout much of the dark phase of the daily cycle. Particular groups were tested always at approximately the same time each day, if there is a circadian rhythm of drinking it is very surprising that no group of animals fell within the optimal period for drinking. Also, in experiments where groups of cockroaches have been observed for twenty-four hour periods (Ewing 1970) no evidence for a daily rhythm of water intake was found.

As cockroaches need very little to drink it was necessary to remove them from the goal box after a maximum of only forty seconds drinking. It is possible that the aversive effects of being handled, although reduced to a minimum, balanced the effects of water reward. However, as with the food reward experiments, animals did not show avoidance of the goal, they showed only random choices. It seems unlikely that the two effects would balance one another exactly under a variety of conditions. The evidence is that the cockroach does not become 'motivated' by water deprivation in the way that many mammalian species do.

7.

EXPERIMENTS WITH ELECTRIC SHOCK AVOIDANCE.

Introduction

The last three sets of experiments have investigated different ways of rewarding the cockroach for making a correct turn in a simple maze. All three techniques, escape from bright light, access to food and access to water, have proved unsatisfactory as reinforcers. In the experiments described below avoidance of electric shock is used to reinforce the learning of positional discriminations in several different designs of simple maze. Research conducted with many species of animal has found a universal dislike of electric shock. It was hoped that punishment by electric shock would finally yield a satisfactory way of producing learnt avoidance behaviour in the cockroach.

Materials

Several different techniques of administering electric shocks were tried out. Initially, an apparatus similar to the shock-grid system used with rats was built. Alternate narrow strips of aluminium foil sheet were connected to the two poles of a variable mains resistor. Another method was tried in which the animal had an electrode implanted in its thorax and stood on a sheet of electrically conducting material. However, the resistive sheet method devised by Longo (1961) was found to be superior to either of these techniques both in simplicity of design and the reliability with which shocks could be administered.

The / .....

/ The resistive sheet consists of a square of cartridge paper thinly coated with 'evostik' glue and sprinkled with powdered graphite. This thin layer of graphite conducts electricity but has a high resistance. Contacts are made along two edges of the sheet by stapling a wire wrapped in aluminium foil along the edge of the paper. The two contacts are connected to the outputs of a variable mains resistor. When a cockroach is placed upon the graphite sheet it is in parallel with the piece of sheet upon which it is standing. As the graphite layer has a high resistance per unit of its area a substantial proportion of the current will flow through the cockroach when the supply is turned on. The animal cannot escape shock posturally (as by arranging its feet on grid bars of the same polarity), nor can it short out the system by producing fluids.

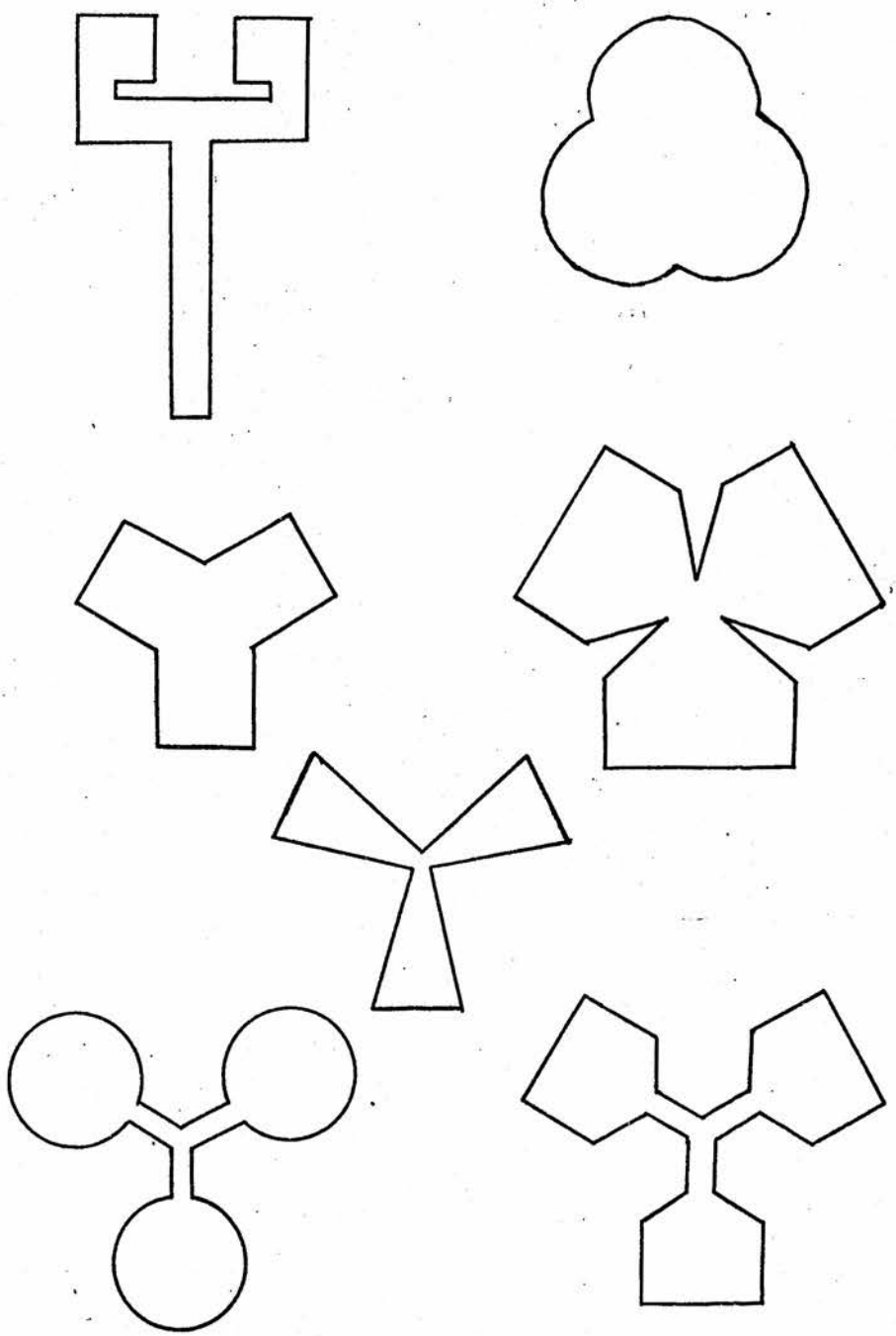
Shock onset was controlled by a tapping contact. Shock was always given intermittently as 'taps' once every two seconds and the voltage level adjusted to the minimum necessary to be aversive to the animal. At very low levels of shock the cockroach may show slight postural re-adjustment but will not move away from the area. At a slightly higher level, the cockroach shows a 'twitch' when it receives the shock and then immediately runs away. At still greater shock intensities the animal leaps into the air as soon as the shock comes on. The level of shock was always kept adjusted so that the animal ran away immediately but did not show a convulsive leap If the animal is already moving when it receives shock it may run forward faster or stop, this depends very much upon the situation.

Several / .....

FIGURE SIX.

COCKROACH MAZES

1/4 actual size



/ Several designs of T- and Y-maze were tried, the complete set is shown in figure six. Each maze was placed on a resistive sheet so that electric shock could be given anywhere in the apparatus. The mazes had low (9mm.), perspex walls and clear perspex tops so that the animal could not escape shock by climbing upwards. Numerous factors were varied in the different designs of mazes, alley width, goal box size and shape, start box size and shape, angle between arms at the choice point, choice point dimensions etc., in order to find the best conditions for training the cockroach.

Subjects

Animals were collected from the small culture tank and marked with spots of paint so that they could be individually identified. They were returned to the tank between experimental sessions.

Methods

Animals were trained on a simple positional discrimination. To avoid shock they had to leave the start box within thirty seconds of being placed in it and then make a correct turn at the choice point. Training proceeded as follows.

Animals were introduced into the start end of the maze via the special box described earlier. If, after thirty seconds, the cockroach had not started to move through the maze, low-level intermittent shock was given. The train of shocks terminated when the animal started to move but began again if the animal came to rest anywhere in the maze for longer than thirty seconds. If the animal made an incorrect turn at the choice point it was immediately given a single shock. It was then removed from the maze and placed in a small / .....

/ small perspex dish. If it made a correct turn it was allowed to remain in the goal box for three minutes and was then removed and placed in the small perspex dish. The apparatus was then wiped with alcohol and the next trial begun. The inter-trial interval was kept at five minutes regardless of whether the animal made an error or not. All animals received five trials a day. The apparatus was dimly lit by a red, ten-watt bulb placed fifteen inches above the choice point.

Preliminary experiments with the variety of mazes shown suggested that the following points are important if a cockroach is to learn its way through the maze:

a) The alley leading up to the choice point must be narrow and have straight, parallel walls.

b) The choice point must be narrow and the arms must branch from it exactly symmetrically.

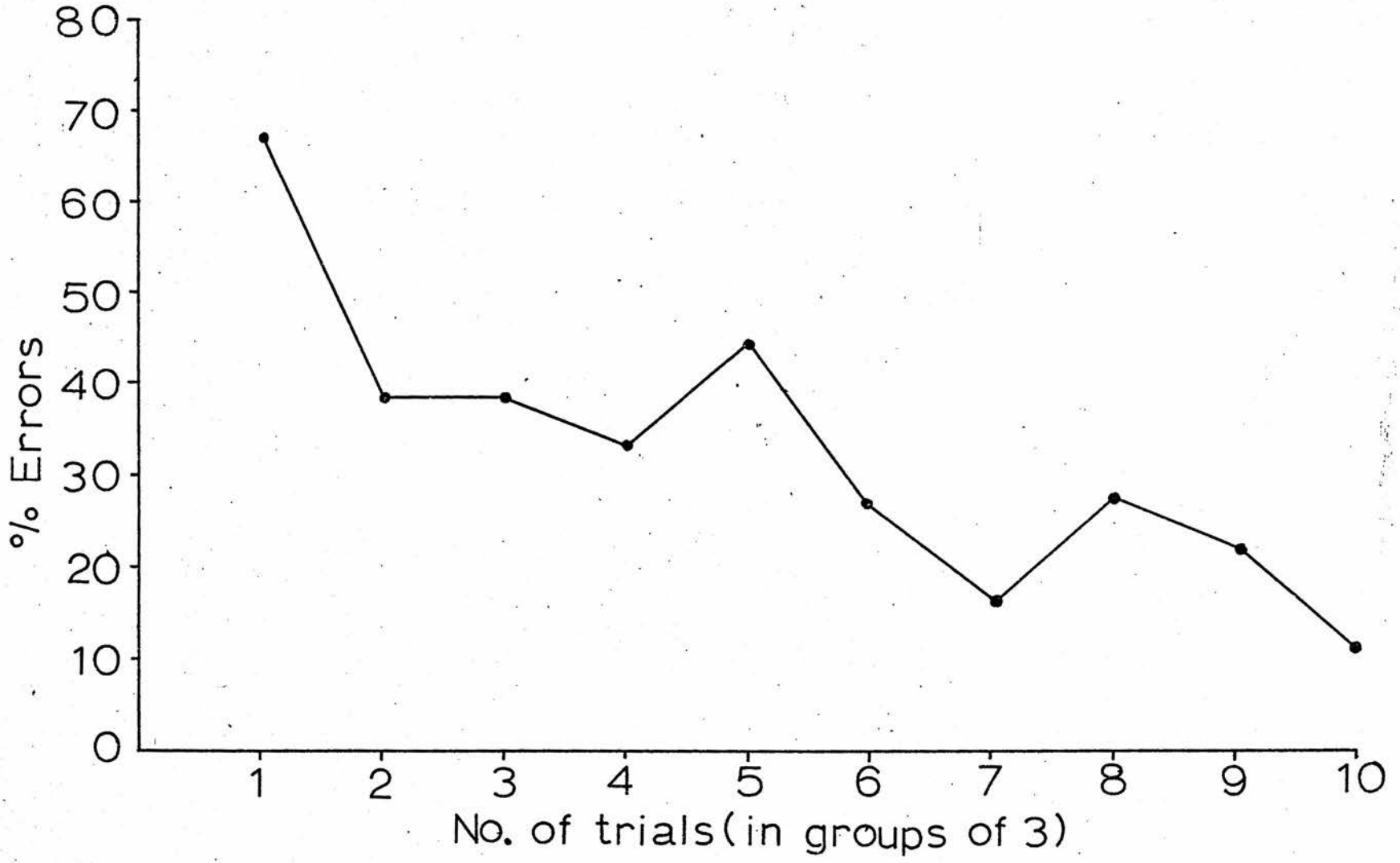
c) The start box must contain as few angles as possible. Otherwise the cockroach tends to try and hide in a corner and avoid shock posturally.

The first two of these points appear related to antennal contact. The best mazes were ones in which the animals were forced to approach the choice point with one antenna touching each wall and when they reached the choice point one antenna went into each of the alternative arms.

Mazes (a) and (f) satisfied the criteria above and both seemed / .....

FIGURE SEVEN.

Learning curve for cockroaches learning a positional discrimination in a Y-maze.



seemed very efficient. No precise quantitative comparison of the mazes was undertaken, the differences between them were so big that it was obvious which mazes were most efficient within a few trials.

Six adult male cockroaches were trained in the Y-maze, (f), according to the method above, until they reached a criterion of five consecutive correct choices.

Results

The results are displayed in figure seven. The percentage errors, averaged for the group of six animals, is plotted against trials. Trials are averaged in groups of three so each point on the graph is a mean of eighteen results. Five of the six animals learnt very rapidly, reaching the criterion of five consecutive correct choices in an average of sixteen trials. The apparatus was easy to use and the behaviour of the animals appeared efficient, after the first few trials animals ran the maze very quickly without any prompting by electric shock, i.e. true 'avoidance conditioning' was observed.

Conclusions

Cockroaches learnt a positional discrimination in a T-maze when punished with electric shock for an incorrect turn or failure to run the maze. The apparatus and method appeared suitable for the study of more complex discriminations.

8.

LEARNING OF AN ACTIVE AVOIDANCE TASK.

Introduction

In the light and shock avoidance experiments the cockroach entered the maze via a special 'introducing box' shown in figure 1. Very quickly the cockroach learnt to leave this box and run into the maze, after the first few trials a cockroach rarely had to be coaxed out of the box by pushing it with the movable wall. Similarly, in the experiments using electric shock animals rapidly learnt not to stay in the straight alley of the maze. These observations suggest that a situation where a cockroach has to learn to avoid a particular area might be an interesting one to investigate.

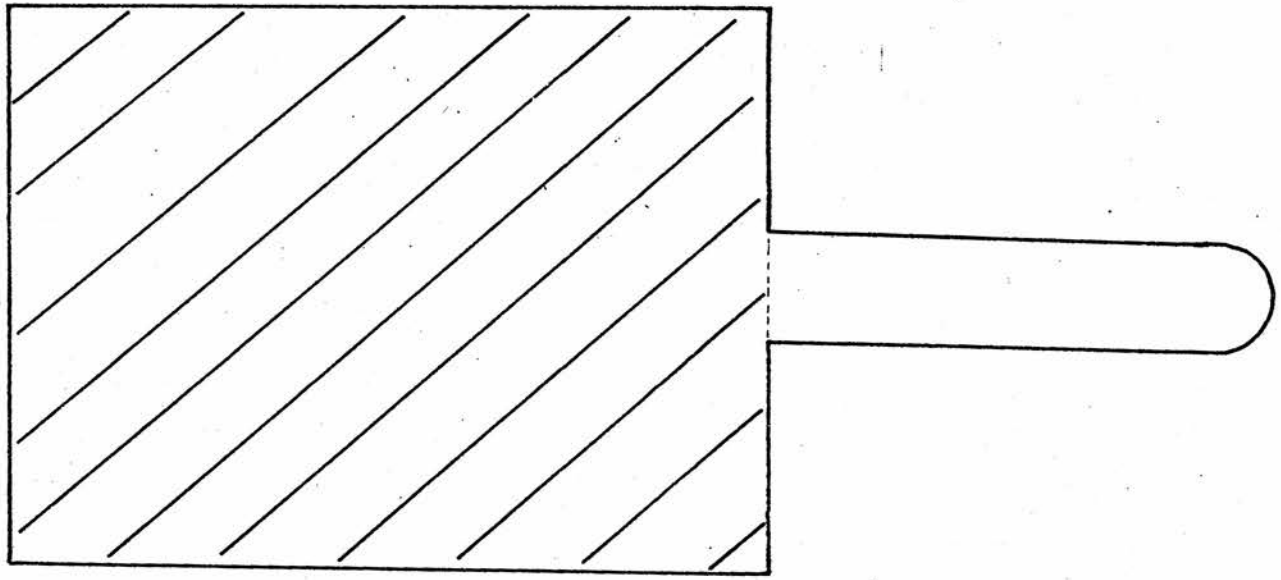
This kind of situation is an example of an 'active' avoidance task. In an active avoidance task an animal has to learn to perform some act in order to avoid punishment, in the example above the animal had to learn to run out of the box and through the maze in order to escape being pushed out of the box or shocked in the maze alley. This situation contrasts with a 'passive' avoidance rewarded task in order to avoid punishment. An example of this kind of situation was given in the cockroach introduction. Animals were trained by Turner to remain in the lighted half of an arena to avoid shock.

The problem studied below is an active avoidance situation / .....

FIGURE EIGHT.

PLAN of AVOIDANCE APPARATUS

ACTUAL SIZE



/ situation very similar to one extensively studied with mammals, particularly rats.

Apparatus

The apparatus consisted of a cardboard box with a small hole at the base of one end wall. This hole led into a plastic vial. The floor plan of the box and vial are shown in figure eight opposite. The box had walls 2 cms high and the vial had a diameter of 1.5 cms. The interior of the box was coated with graphite on Evostik by the method described earlier. Electrical contacts were placed along the tops of the two side walls and connected to a variable resistance, tapping contact and mains supply. Electric shocks could be administered to a cockroach anywhere inside the box, but the plastic vial was a safe area in which no shock could be given.

Subjects

Twenty marked adult male animals were used in the experiments. They were kept in the small culture tank and returned to it between sessions.

Method

The experiment was divided into three parts.

1) Pre-training test. The subjects were divided into two groups of ten animals and each given five pre-training trials. On each trial one animal was placed in the graphited / .....

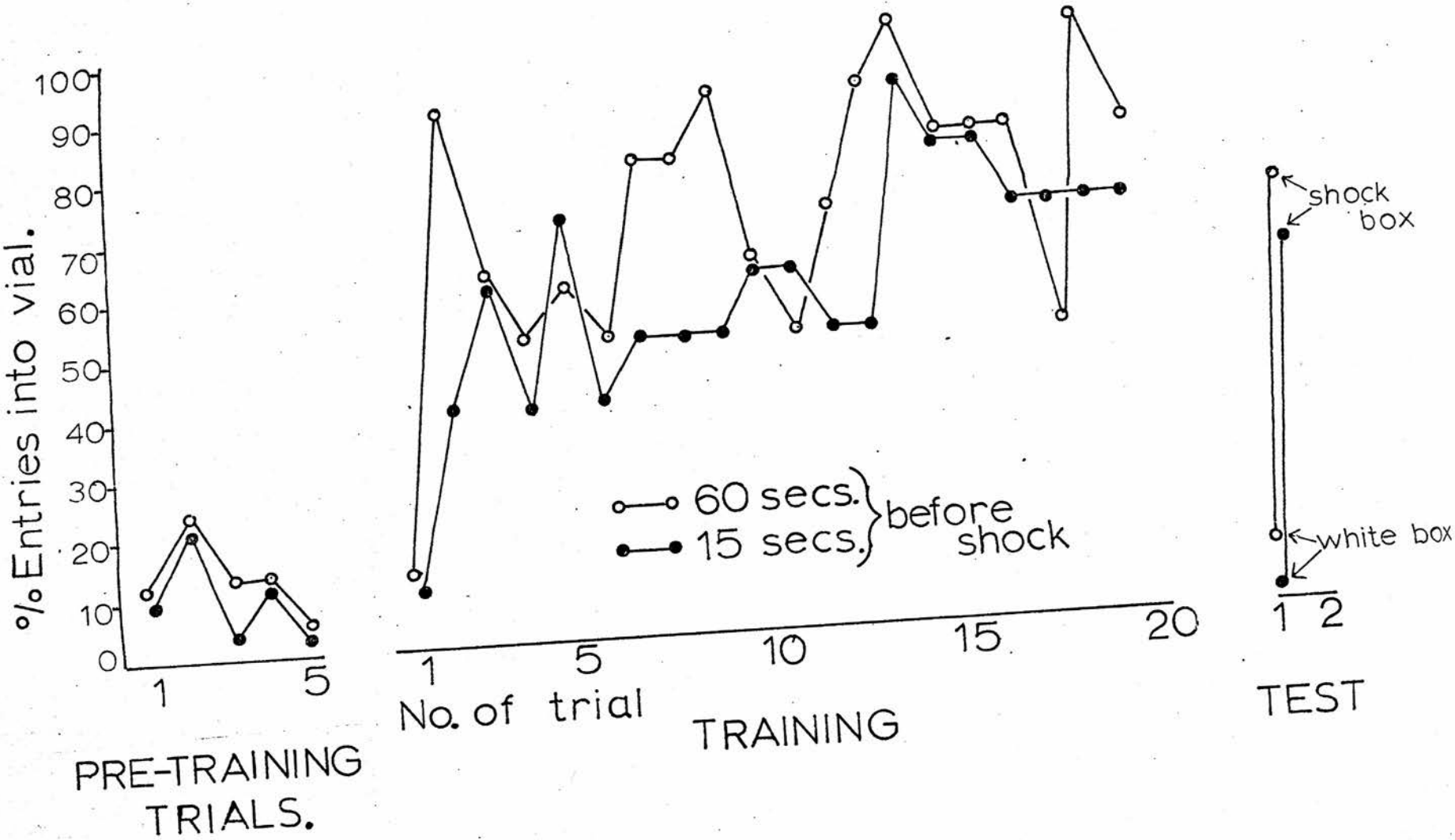
/ graphited shock box and left there for an interval of time. For animals in Group 1 this interval was 15 seconds and for animals in Group 2, 60 seconds. The number of times the animal entered the plastic vial during this period was recorded. At the end of the time interval the animal was removed from the box and left in a clear glass dish for five minutes. This procedure was then repeated for each of the five trials.

2) Training. During the training trials the animals were again placed in the graphited box. After 15 seconds (Group 1) or 60 seconds (Group 2) shocks were given. Intermittent shock at the rate of one pulse per two seconds was used throughout. When the shock came on, the animal's increased locomotion usually resulted in it entering the plastic vial by chance within a short period. If it entered the vial before shock came on then it avoided shock altogether. Once it had entered the vial, the cockroach was left there for five minutes before it was removed and the procedure repeated. Ten such trials were given a day and all animals received twenty trials. On every trial it was recorded whether or not the animal managed to avoid shock altogether by entering the vial before shock came on.

3) Post-training test. At the end of the twenty trials animals were given an additional two trials. Firstly, instead of being placed back in the shock box which, being coated with graphite, is jet black, they were placed in an identical white cardboard box. The number of animals leaving the box was recorded in the usual fashion. The animals were / .....

FIGURE NINE.

Learning curves for cockroaches learning to avoid an area in which they have been shocked.



/ were then returned to their culture tank for 24 hours. Finally, they were given a trial in the shock box according to the usual procedure.

Results

The animals learnt to avoid shock by running out of the box into the vial in the period before shock came on. The percentage number of animals entering the vial is plotted against trials in figure nine. The two groups are plotted separately. As each group contained ten animals a score of 100 per cent would imply that all ten animals ran out of the box on that trial. During the pre-training period the animals showed little inclination to enter the plastic vial. However, after receiving shock in the black box with successive trials there is a rapidly rising tendency to leave the box. Even on the second trial ninety per cent of the animals in Group 2 successfully avoided punishment. In Group 1 thirty per cent of the animals avoided shock on the second trial. A great change in the animals' general behaviour was also noted. During the pre-shock trials the animals either stood still or moved around the box in a slow exploratory manner. After having only one shock period the cockroaches showed 'high arousal' when subsequently placed in the box. Their antennae began to wave furiously a few seconds after being put down and then they began to run around excitedly. This excitement was seen even in animals which did not succeed in successfully finding their way out of the box.

The / .....

/ The post training trials show that this learnt avoidance of the box is specific to the training apparatus and that it is retained for at least 24 hours. When placed in the white box (Test 1) the animals showed no tendency to escape from it although when placed in the shock box 24 hours later (Test 2) they demonstrated a high level of avoidance. These controls were necessary because it was possible that the effect of shock was simply to sensitize the animal to run when any stimulus occurred. The stimulus of being handled by the experimenter while being placed in the box may have been sufficient to set off a burst of activity in a sensitized animal. However, no activity occurred in a white box but the avoidance behaviour in the black box is still present 24 hours after last receiving shock.

Conclusions

Cockroaches show a marked increase in escape from a small black box after they have received electric shock in it. This change in behaviour takes place extremely rapidly and control experiments show that it is not due to a sensitization effect. One other possibility must be ruled out before it can be claimed that the change in behaviour is truly learned. It is possible that the animals release an alarm pheromone when shocked and that this causes the increased escape activity in the box on subsequent trials. However, this possibility is extremely unlikely as the cockroaches were trained consecutively in the same apparatus but each animal showed the same sequence of changes in behaviour. It thus seems certain that this experiment demonstrates / .....

demonstrates true avoidance conditioning.

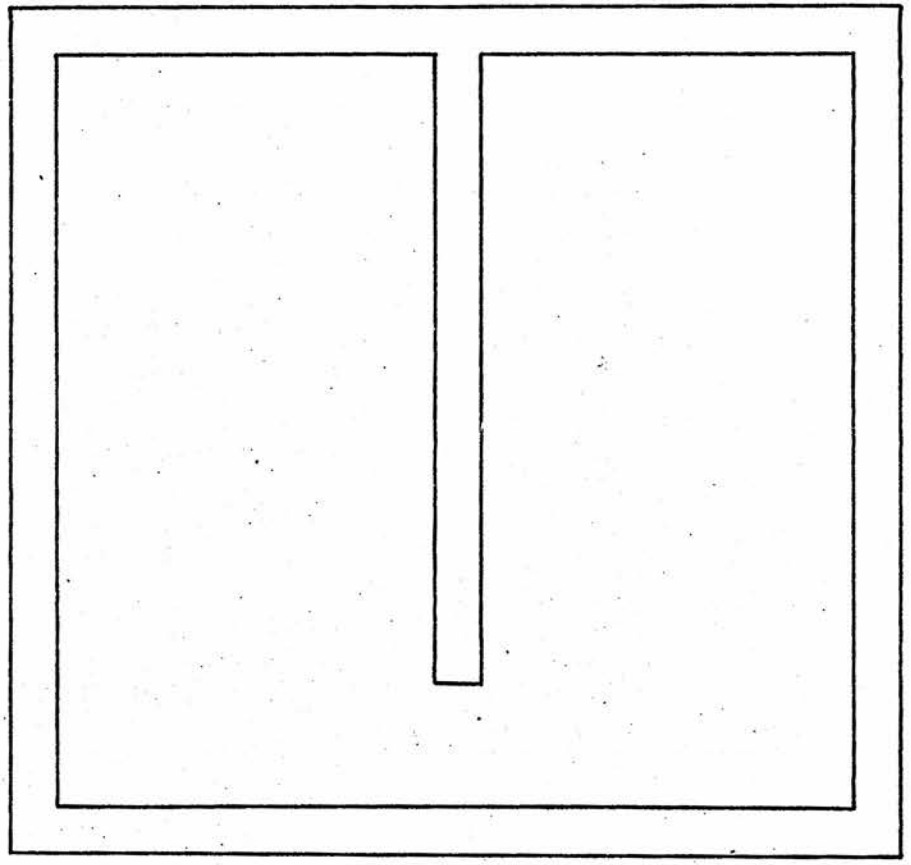
It is remarkable that cockroaches are able to learn to avoid punishment in this apparatus in only one trial. Part of the explanation for this might be that the plastic vial is 'a good place to hide'. It is of small diameter and is rather similar to the kind of cracks a cockroach normally hides in when it is frightened. The behaviour of the cockroach on this task is not inferior to that of the rat. In later experiments the complexity of this problem is increased in an attempt to find the limits of the cockroaches' learning capability.

9.

LEARNING IN THE SHUTTLEBOX.

FIGURE TEN.

PLAN of SHUTTLEBOX (ACTUAL SIZE)



Introduction

The last section showed that cockroaches are remarkably efficient at solving a simple avoidance task. Indeed, they perform no worse than rats in a similar situation. In order to find out more about the limits of the cockroaches learning capabilities a more complex avoidance situation was developed from the first. The situation is analogous to the 'shuttlebox', a piece of apparatus commonly used by mammalian workers.

The shuttlebox usually consists of two identical compartments separated by a low barrier. If shock is turned on in either compartment the animal can escape from it by jumping over the barrier to the other compartment. Before the shock is turned on a warning stimulus is given; if the animal responds promptly to the warning stimulus by crossing to the other side then it will avoid shock altogether.

The behaviour of the rat in the shuttlebox has been extensively studied. On the first few trials, when the shock is turned on the rat runs around until by chance it passes into the other end of the shuttlebox and escapes shock. As training proceeds the animal learns to escape shock more efficiently by 'hurdling' the barrier as soon as the shock is turned on. However, at this early stage it still does not avoid shock altogether by escaping when the warning stimulus comes on. Next, there commonly occurs a phase in which the rats spontaneously cross to the other side of the shuttlebox / .....

/ shuttlebox in between trials without having been shocked and before the warning stimulus is given. About the same time the animal begins to make some successful avoidances. It would appear that at this stage the animal has learnt that it must escape but has not learnt to discriminate between the 'situation-with-warning-stimulus' and the 'situation-without-warning-stimulus'. It thus runs rather indiscriminately as it has not properly learnt that the warning cue signals the onset of shock. Another way of putting this (after Mowrer 1960) would be to say that the animal has developed fear of the situation as a whole and knows how to reduce fear (by running to the other side) but has not learnt to attach fear specifically to the situation-with-warning-stimulus. Eventually the rat learns this discrimination and runs only when the warning stimulus comes on, it now attachs fear specifically to this cue.

This problem has increased in complexity in several ways compared with the simple, active, avoidance situation described in the last section. In the simple situation one part of the apparatus was associated with shock and another with safety from shock. The 'shock' area and the 'safe' area were clearly distinct and differed from one another in size, position and tactile properties. In the shuttlebox there is no distinct 'safe' area, shock may be received anywhere in the apparatus. Instead of learning to run from a particular place animals must learn to respond to a specific warning cue independent of position.

The / .....

/ The behaviour of one species of insect, the house-cricket Acheta domestica, has been studied in an avoidance situation similar to that described above (Robert 1967). In this experiment an arena was divided into two parts, half dark and half light. Crickets were trained to confine themselves to the dark side of the arena by giving them electric shocks if they stepped into the light side. Every three minutes the light and dark sides were reversed and the animals could avoid shock by responding to this signal and crossing over to theother side so they were once more in the dark. However, although crickets learnt to escape the subsequent shock efficiently they never learnt to avoid shock by using the inversion of the lighting as a cue. Robert concludes about this failure "il est plus difficile pour les Grillons".

Materials

The cockroach shuttlebox had the floor plan shown in figure ten and was built of perspex. The shuttlebox was divided into two compartments by a barrier. The cockroach could pass from one side to the other through the small opening at one end of the barrier.

The shuttlebox was placed on a resistive sheet so that shock could be given anywhere in the apparatus. The walls were low (nine millimetres) so that the cockroach could not escape shock by climbing up the walls. On top of the apparatus was placed a clear perspex lid. It was marked out with a grid of one inch squares so that the distance moved by the cockroach / .....

/ cockroach could be measured. The apparatus was lit by a red, ten watt bulb placed fifteen inches above its centre. The stimuli used as warning signals were light onset and vibration of the floor. The floor vibration was provided by means of an electric bell clamped to the bench alongside the shuttlebox. The bell was modified so that the hammer struck the bench instead of the bell. The frequency of vibrations was measured with a stroboscope and kept constant throughout the experiment. The light-onset cue was produced by switching on a 60 watt bulb eighteen inches above the centre of the shuttlebox. The cockroach obviously detected both of these stimuli as it usually showed some response to them even after many trials in the apparatus.

Subjects

Fourteen adult male cockroaches were collected from the small culture tank and marked. They were taken out of this tank for training and returned to it afterwards. Unfortunately, two animals escaped from the tank shortly after the beginning of the experiment. Results are reported here for only twelve animals.

Methods

An animal was placed in the shuttlebox and left for one minute to accustom itself to its surroundings. The warning cue was then given and afterwards the shock turned on. Shock was terminated as soon as the cockroach passed through the opening in the barrier. Shocks were given as intermittent pulses at the rate of one every two seconds. The train of pulses was stopped if the cockroach was moving and re-started only / .....

/ only if the animal came to rest without having passed through to the other side. Shock was always kept to the minimum necessary to produce escape behaviour. There were three conditions of warning stimulus/shock onset:

A: Four animals received light on, four seconds delay, shock on.

B: Six animals received vibration on, four seconds delay, shock on.

C: Four animals received vibration on, two seconds delay, shock on.

Preliminary experiments had shown that the cockroaches sometimes crossed over from one side to the other during the inter-trial interval. Half of the animals in each of the three groups above were allowed to cross over during the inter-trial interval. This Group is referred to as Group I. The other animals, Group II, were punished if they attempted to cross over during the inter-trial interval. As their heads passed through the opening in the barrier they were given one electric shock.

All animals received ten trials a day. The inter-trial interval was three minutes and each animal received a maximum of 250 trials.

Nine sources of behaviour were recorded throughout the training sessions. Although psychologists commonly record only error scores in learning situations, measuring many different behaviours helps to give a better idea of what an animal learns about a particular situation. The nine measures / .....

/ measures of behaviour taken are described below.

1) It was mentioned previously that the apparatus was marked off into inch squares. The total number of lines crossed by the cockroach during each trial was measured and is referred to as escape distance. The animal was considered to have crossed a line only if its body completely passed from one square to another.

2) When electrically shocked a cockroach normally runs off forwards. If the animal turned through more than 90 degrees and towards the opening in the barrier when first shocked then turn was scored.

3) If the animal ran through the barrier opening and came to rest within one inch of it then near was scored.

4) If the animal crossed to the other side but then immediately, without stopping, ran back into the shock side then re-entry was scored. When an animal did this it would once more be shocked as it re-entered the side it began from.

5) Postural avoidance of shock was scored. This usually took the form of attempted wall climbing or huddling up in a corner.

6) If the animal was running towards the opening in the barrier but when within one inch of it suddenly turned away and did not pass through then refuse was scored.

7) If the animal was more than two inches from the barrier opening / .....

/ opening and ran through on the first shock it received, then continue was scored.

The final two scores were of behaviour seen during the inter-trial period.

8) Approach was scored when the animal oriented to the barrier opening and was within one inch of it. Although this behaviour pattern frequently preceded spontaneous crossing the animal often appeared to wait in this position until it received a shock and then passed through the barrier opening.

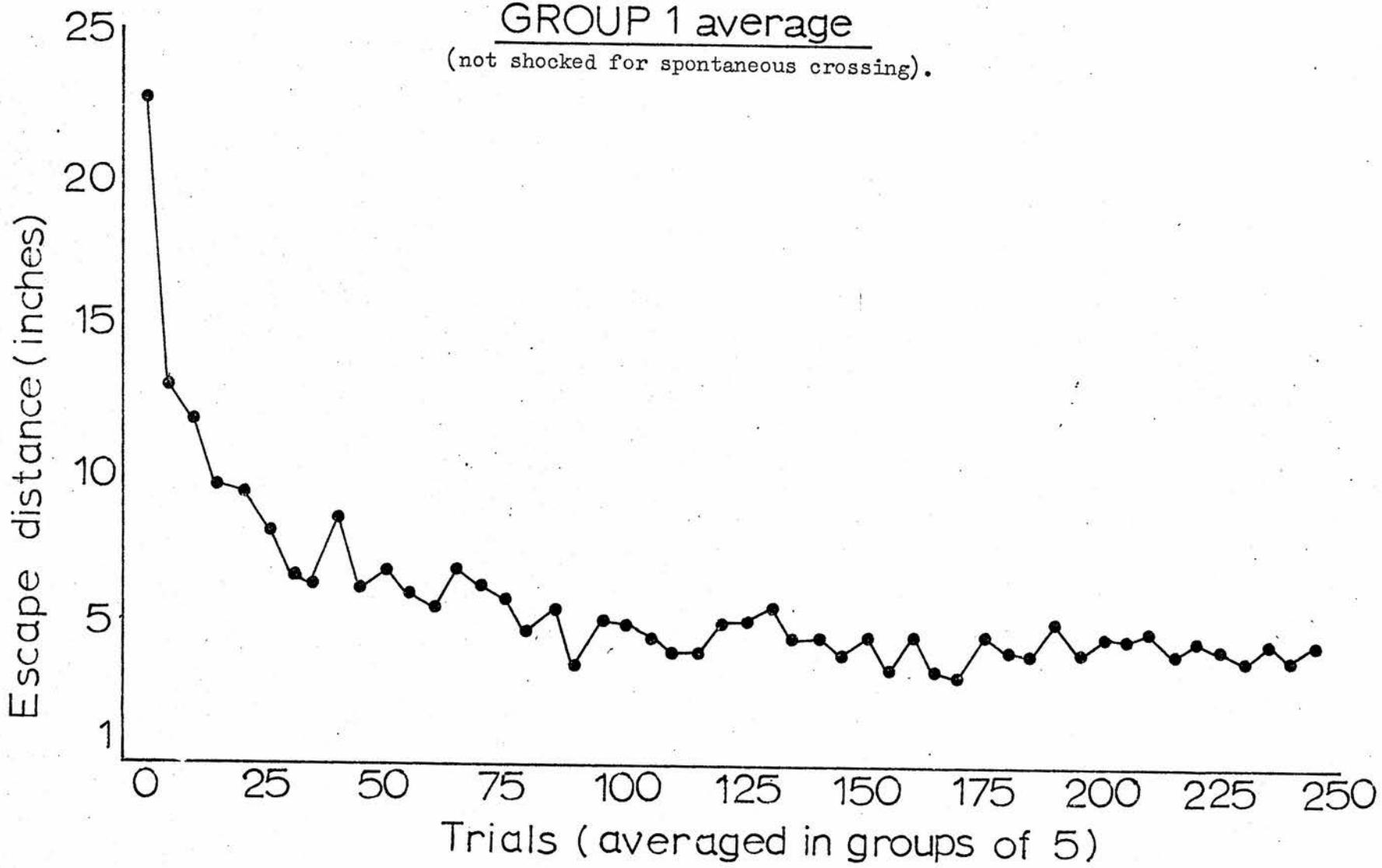
9) Spontaneous crossing was scored if the animal crossed over to the other side. This pattern was frequently preceded by the previous one or by exploration of one side of the apparatus. It was quite different from re-entry which took place when the animal ran straight into one side and straight back out again. Spontaneous crossing took place as a slow exploratory walk during the inter-trial interval.

Results

At no time did escape behaviour occur before the first shock; thus none of the animals ever learnt to avoid shock by crossing over in the period between the warning signal and shock onset. This applied to all the groups tested. There were no differences in behaviour towards the warning stimulus between any of the different groups. In all cases, although the cockroach might show a slight postural re-adjustment or movement of the antennae when the warning stimulus came on

(its / .....

FIGURE ELEVEN.



/ (its normal 'orientation reflex'), it never showed any locomotion or escape behaviour to this stimulus.

However, some very interesting changes in behaviour were seen. In particular the two groups divided on the basis of no punishment (Group I) and punishment (Group II) for spontaneous crossing, showed quite different results.

These results will be considered in some detail.

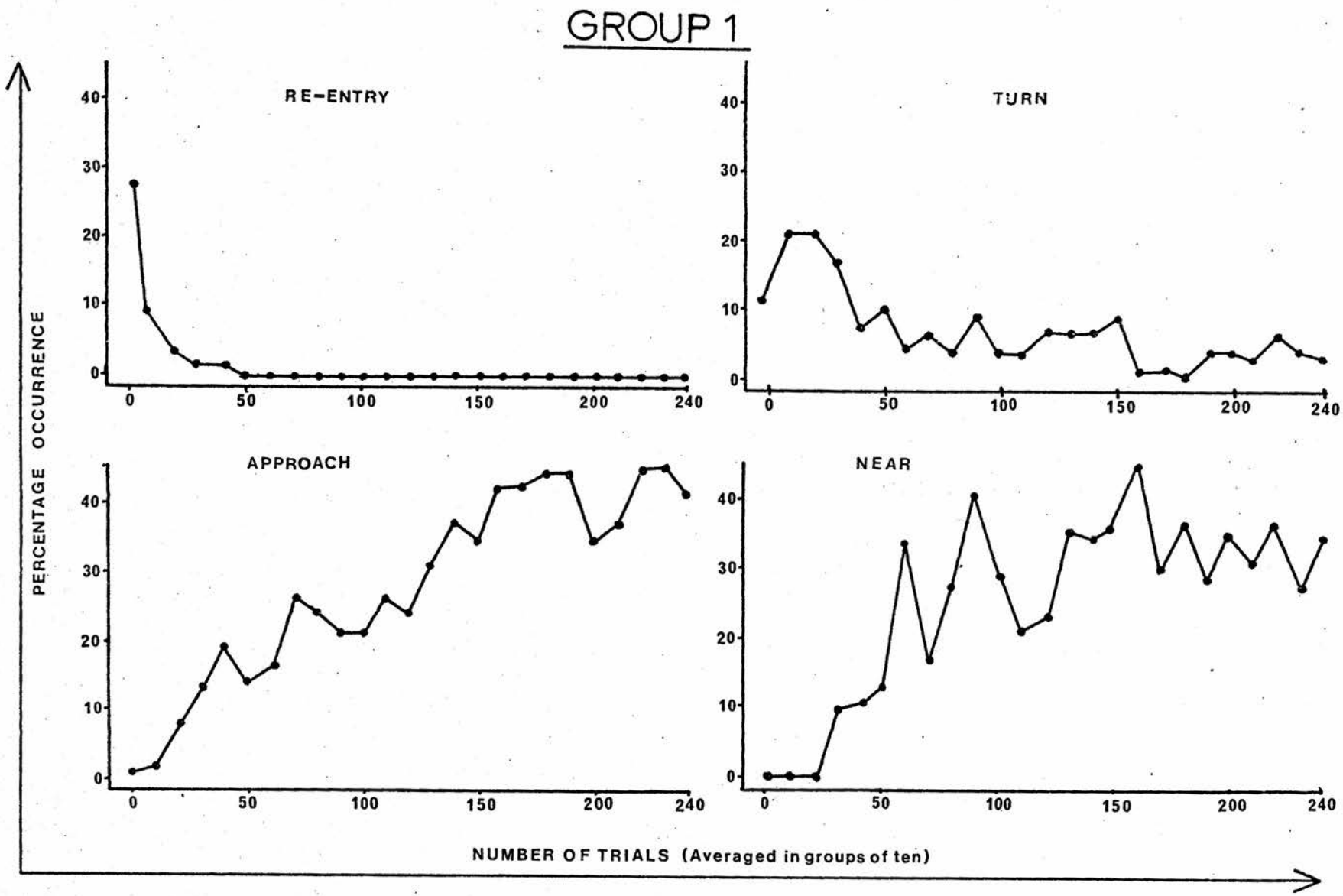
Group I - animals unpunished for spontaneous crossing.

Although these animals did not learn to avoid shock they did learn to escape shock much more quickly. The curve shown in figure eleven is a graph of escape distance against trials. Results are treated in groups of five. Each point on the graph represents the mean of seven animals escape distance over a set of five trials. Each point is thus an average of thirty-five separate results. The curve shows that, with trials, the animals learnt to run a much shorter distance to escape shock. Their running became better directed and was no longer random.

This change in behaviour may be analysed in more detail by reference to the other behavioural scores. These are plotted in diagrams 12 and 13. Each curve shows the percentage occurrence of that behaviour pattern against trials averaged in blocks of ten. Percentage occurrence is the total number of trials (from all seven animals) on which the behaviour pattern occurred divided by the total number of animal.trials multiplied by a hundred. Percentage occurrence is calculated for each block of ten trials. Taking the behavioural graphs in turn:

1) / .....

FIGURE TWELVE.



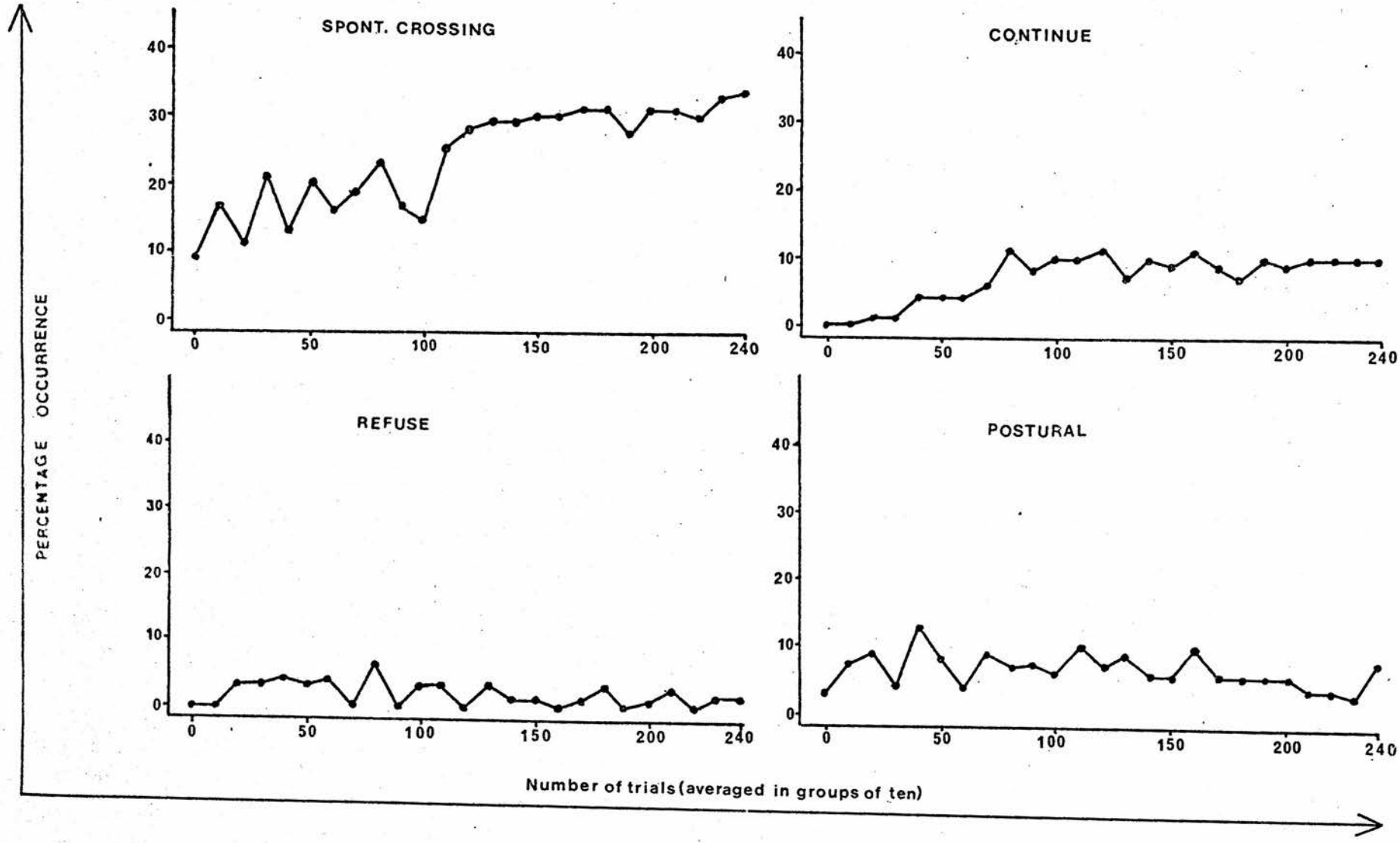
/ 1) Re-entry showed an initial sharp decrease in frequency reaching zero by trials fifty to sixty and never re-appearing thereafter. This drop was in phase with the first steep drop in escape distance. The initial change in escape distance may be due to the inhibition of re-entry into the shock side of the apparatus. This is a very marked change, for on the first few trials the animal showed a 'panic reaction when shocked and ran wildly all over the place.

2) At the same time that re-entry was showing a sharp fall, turn showed a sharp increase reaching a peak in trials ten to thirty and then gradually falling away during the rest of the experiment. This showed that the animal was orientating to the barrier opening when shock came on, i.e. it had learnt a much more specific response to shock than just running. The cockroach had thus learnt something of what to do about shock. The fall in turn can be accounted for in terms of the rise of approach.

3) Approach showed a gradual rise beginning in trials ten to twenty. In the final part of the experiment, at the beginning of approximately forty per cent of trials the animal was oriented to the gap and within one inch of it. This behaviour made low escape distance and concomitant low exposure to shock inevitable. Also as approach and turn cannot both occur on the same trial, then turn fell as approach rose.

4) Near began to rise in trials 30 to 40 and reached asymptote / .....

GROUP 1 (contd)



/ asymptote by trial 80. After trial 80 the animal was stopping after passing only one inch or less through the barrier opening on approximately 30 per cent of trials.

Considering these last two scores together it can be seen that the cockroach had learnt a highly efficient means of escaping shock in the minimum time. It waited near to the barrier oriented in the right direction and then moved only just through when it was shocked. It then re-oriented during the inter-trial interval.

5) Spontaneous running showed an increase over the first 110 trials and then remained at a stable level. As pointed out earlier, rats also show this behaviour in the shuttlebox. However, cockroaches never learnt to run specifically to the warning stimulus.

6) Continue showed a gradual rise but only ever reached a low level. Thus the cockroach never learnt to consistently avoid further shock by escaping on the first shock it received. This suggests that it is very difficult for the cockroach to learn to avoid shock even when shock is the cue signalling further shock.

7) 8) Postural avoidance and refuse maintained a stable low level throughout the experiment.

These results suggest that although the cockroach can learn to associate shock with the apparatus generally and learn to escape shock it cannot learn to discriminate between the situation-with and the situation-without warning stimulus.

<u>Group II</u> /.....

FIGURE FOURTEEN A.

Average escape distance plotted against trials for animals in Group II, the group punished for spontaneous crossings.

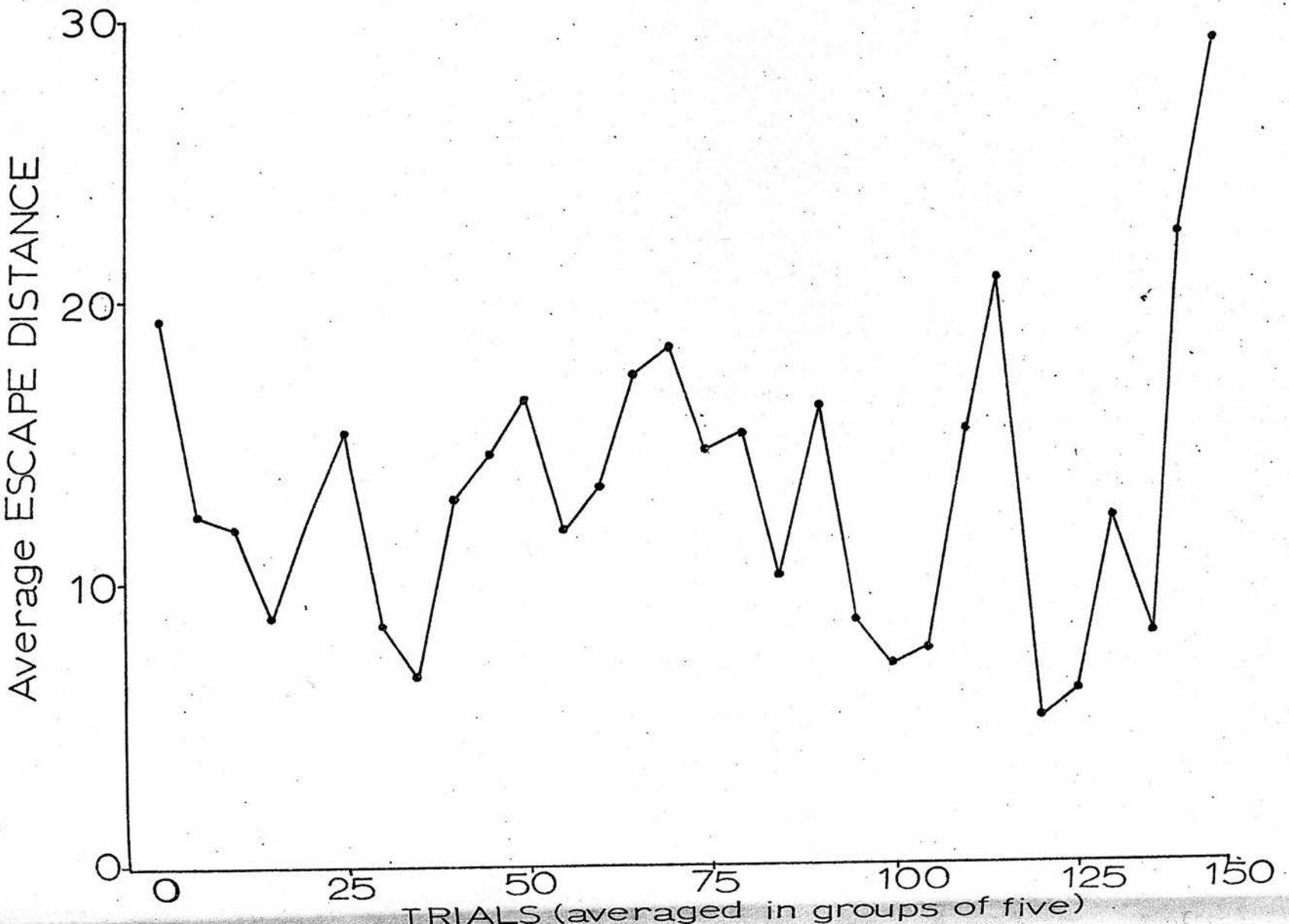
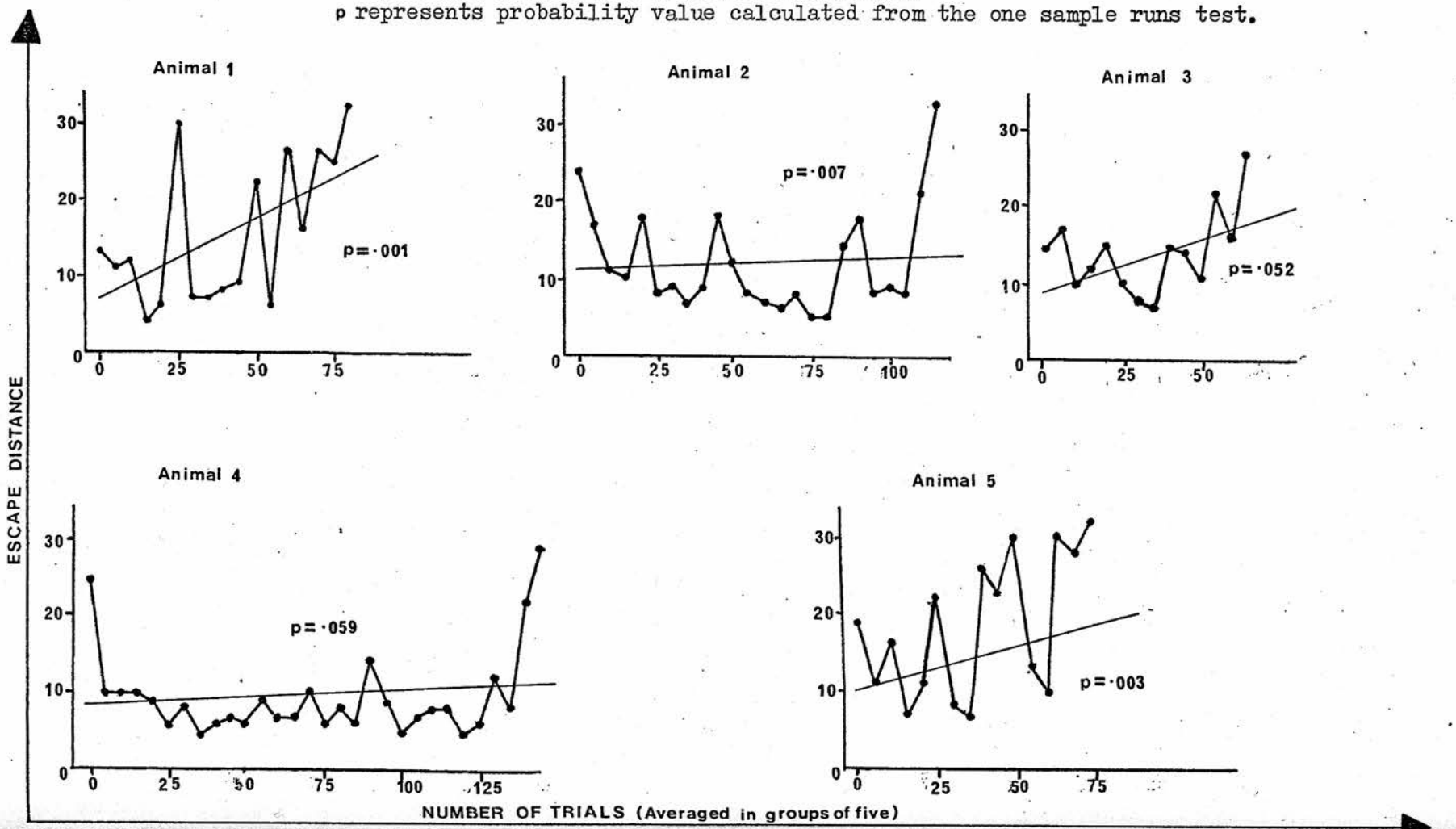


FIGURE FOURTEEN B.

Escape distance plotted against trials for the 5 animals in Group II

——— represents line fitted by linear regression.

p represents probability value calculated from the one sample runs test.



Group II - animals punished for making spontaneous crossings.

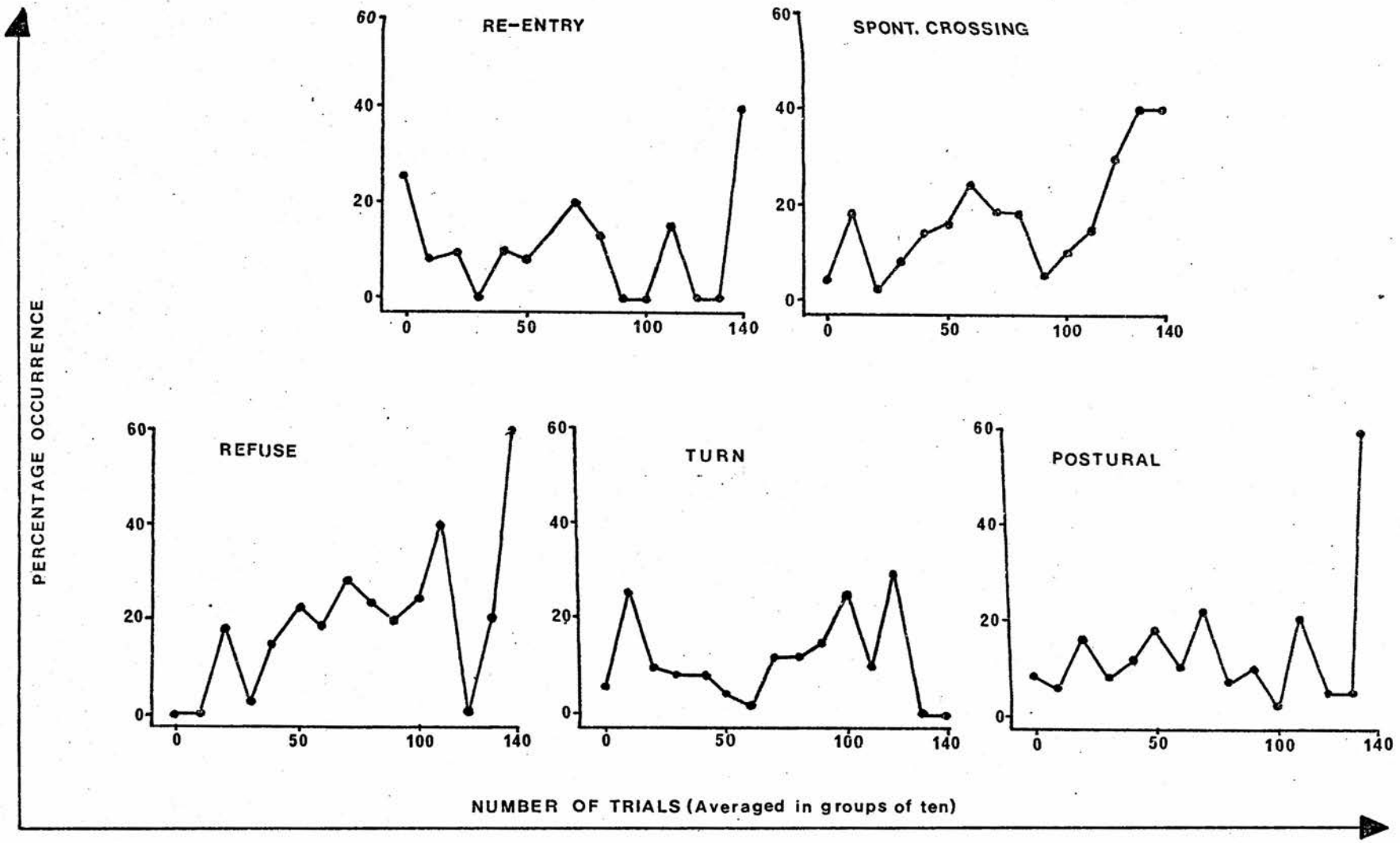
The average escape distance is plotted against trials in figure fourteen A. The results are the average of all five animals in the group for blocks of five trials. Each point on the graph thus represents the mean of five animals escape distance over a set of five trials. It can be seen that unlike the results found for Group I (figure eleven), there is no consistent tendency to reduce escape distance and after 150 trials animals are performing no better than they did initially.

Individual graphs for each of the five animals in Group II are plotted in figure fourteen B. In the graphs escape distance, averaged over five trial blocks, is plotted against trial blocks. In all these individual graphs it can be seen that over the first few trials escape distance fell. However, instead of falling to a consistent low level this initial decrease was followed, after a variable period, by rises and falls in escape distance culminating in distances so great that shock continued for minutes. Training was terminated at this point as these long periods of shock were clearly beginning to injure the animals.

The fluctuations in escape distance are not simply due to the animals behaving randomly but rather they show alternate phases of high and low escape distance. This was demonstrated statistically. Firstly, a straight line was fitted to the results of each individual by standard techniques of linear regression. If the variable results were simply due to the animals behaving randomly then it would be expected that points would lie above or below this line in a random order. However, when the serial order of 'high' and 'low' results is examined (according to whether they lie above or below the regression line) and compared with theoretical distributions by means of the One Sample Runs test (Siegel 1956) it is found that the results are not random. A significant number of runs of 'high' followed by 'low' results occurs. P-values which reflect the probability that the order of results

FIGURE FIFTEEN.

GROUP 2



is due to chance variation are shown alongside each graph in figure fourteen B. On the basis of the behavioural scores taken a possible explanation for the presence of rises and falls in escape distance is suggested. Further statistical details are given in Appendix I.

The full range of behavioural scores is plotted in figure fifteen opposite. Once again the percentage occurrence of the behaviour pattern is plotted against trials in groups of ten. Considering these scores in turn :

1) Re-entry showed an initial drop accounting for the initialsharp drop in escape distance. Shortly afterwards it rose again in phase with the increases in escape distance. Once again the animal began to run back into the shock after having escaped from it.

2) Spontaneous running also showed a sharp increase in phase with the increase in running distance, even though every time these runs are punished by more shocks.

3) Postural avoidance also rose to high levels, frequently the animals would freeze up in a corner and not move even when given shocks.

4) Turn showed an initialincrease as in the first group, but then it rose and fell out of phase with the increases in escape distance. Thus, during phases of low escape distance the behaviour of the cockroach showed that it had learnt something about to escape from shock.

5) Refuse, which in the first group remained at a constant low level throughout the experiment, rose to extremely high levels in phase with the increases in running distance. Every increase in escape distance was associated with an increase in the refuse score.

6) 7) and 8) Approach, near and continue were seen scarcely at all and are not plotted.

It appears from the above results that the animal initially decreased its running distance in the same manner as the first group. It initially stopped re-entering the shock side of the apparatus once it had succeeded in making an escape. However, when spontaneous

/ However, when spontaneous crossings developed and were punished the cockroach began to avoid the place where it received punishment, in this case the opening through the barrier. This particular point provided unique tactile cues and might have been very easily recognised by the cockroach. Avoidance of this spot caused the animal to turn back when it approaches the barrier opening (seen as the rise of the refuse score), so that it received still more shock as it circled one side of the apparatus. This seemed to lead to a 'panic' in which the animal displayed high postural avoidance or ran to the other side and then ran straight back into the shock side again.

As spontaneous running was punished and avoidance of the barrier opening increased, spontaneous running was itself suppressed. Shortly after spontaneous running ceased, avoidance of the barrier opening also fell to zero. Once more the cockroach began to successfully escape shock. However, after a varying period spontaneous running began again, it was punished, the refuse pattern was again seen and the whole cycle repeated itself. In the individual escape distance curve plotted in figure fifteen there are four peaks of high escape distance, the final one being too high to permit further experimentation.

If we look at this behaviour in the terms used by Mowrer (1960) in discussing avoidance conditioning in the rat, it would appear that the cockroach develops a fear of the place where it was shocked and learns to reduce the fear by running to the other side. However, because it has been shocked generally in the apparatus it begins to show spontaneous fear-reducing 'escapes'. These are punished and the cockroach now begins to fear the place where it was shocked, the barrier opening. / .....

/ opening. The cockroach then becomes caught in a conflict situation in which fear of the apparatus or shocks tells it that it must run to the other side while fear of the barrier opening tells it to stay where it is. The rise and fall of escape distance reflects the relative strength of these two fears. Escape distance rises as the tendency to avoid the barrier opening pre-dominates and falls as the tendency to 'escape' and run to the other side pre-dominates. The cockroach does not learn that it is correct to run at certain times (when the buzzer/light sounds) and not currect at other times. The cockroach is responding to the apparatus situation as a whole and not to the specific cue which must govern its behaviour if it is to consistently avoid shock.

A similar conclusion is reached from the consideration of the animals in Group I. Although up to a point the animal behaves in a manner similar to that of the rat it never makes the final step of learning to respond to the buzzer instead of the situation as a whole. In learning to avoid shock animals have to learn to pay attention to the relevant warning stimulus cue and ignore place cues. Learning to respond to the warning stimulus cues and not the the same situation without warning stimulus appears beyond the ability of the cockroach. It has already been mentioned that work with another insect, the cricket, came to an identical conclusion.

It might well be argued that if the conditions were changed, stimuli perhaps changed, apparatus modified etc., the cockroach (and the cricket) would finally have solved this problem. A negative result can always be answered in

this / .....

this way. Although in this situation the Group I animals seem to come to a stable conclusion (their behavioural scores had been at asymptote for a hundred trials) it is possible that further training would have produced a different result. However, while no attempt was made to repeat this experiment under different conditions, experiments in which similar factors paly a part will be found in the next section.

10.

DISCRIMINATION, DISCRIMINATION-REVERSAL AND CONDITIONAL DISCRIMINATION TASKS.

Introduction

In the general introduction to this thesis a considerable amount of space was devoted to the discussion of comparative studies of reversal learning. In this section the bheaviour of the cockroach on a reversal learning task and a conditional reversal learning task is described. Their behaviour is compared with that of other animals on similar tasks.

A pilot experiment was first carried out to find suitable cues for use in the reversal learning experiments.

Experiment A: The discrimination of single cues in a Y-maze.

Introduction

In this experiment the cockroach was trained in a Y-maze situation similar to that already described in Section six. However, instead of the animals learning a simple left/right positional discrimination they had to learn to discriminate certain specific cues. Groups of animals were trained to discriminate three kinds of cues; direction of air currents, light/dark and presence/absence of odour. These cues were chosen because it seemed likely that the cockroach would be able to detect them. Previous experiments have already shown that the cockroach can respond to differences in light intensity. Both antennae and cerci are known to be sensitive to mechanical disturbance so it seemed probable / .....

probable that the animal would be able to detect differences in air currents. The cockroach is known to respond to a number of odours.

Apparatus

The apparatus consisted of a Y-maze identical in floor plan to that seen in figure five. It was built of perspex and its walls were one centimetre high. Air tubes led into the two goal boxes and the start box and a close fitting perspex lid made the apparatus air-tight. The Y-maze was placed on a resistive sheet connected to a variable mains resistor so that electric shock could be given anywhere in the apparatus.

The three stimuli were provided as follows.

a) Air currents. The air tube leading into the start box was sealed and an electric pump connected to one of the goal box air outlets. When air was sucked from here it entered through the air tube in the other goal box. Thus, by connecting the pump appropriately it was possible to have a flow of air going in either direction through the goal arms across the choice point.

b) Light intensity. The two arms leading to the goal boxes could be unequally illuminated. A bulb and lens threw a parallel beam of light onto the maze. A shaped piece of black cardboard held in a burette stand was positioned so that the light fell on only one of the arms. The position of the lens and masking card could be arranged so that the light/dark boundary was sharp and exactly bisected the choice point area. / .....

/ area. The intensity of illumination was set at a value that initially was neither attractive nor aversive.

c) Odour. Air was drawn through the start box outlet by an electric pump and entered through the goal box inlets. Each inlet hole was attached to a small perspec pipe. In one pipe was placed a small drop of a dilute solution of oil of lavender. In the other was placed a small drop of water. Scented air flowed from the lavender tube down one arm of of the maze and into the start alley. Clean air flowed from the other arm.

In all three situations a red ten-watt bulb provided light over the whole apparatus.

Subjects

Fifteen adult male Nauphoeta cinerea were individually marked and kept in a small culture tank. Each had a small cotton loop waxed to its thorax.

Methods

The animals were divided into three groups each of five animals. Each group was trained to discriminate one kind of cue. Group A was trained to discriminate light/dark. The animals were rewarded for turning into the lighted arm of the Y-maze. Group B was trained to discriminate the direction of air currents. Animals were rewarded for turning upwind at the choice point, i.e. into the arm from which air was flowing.

Group C was trained to discriminate presence/absence of odour. Animals were rewarded for turning into the lavender scented arm. In all cases the position of the correct arm was / .....

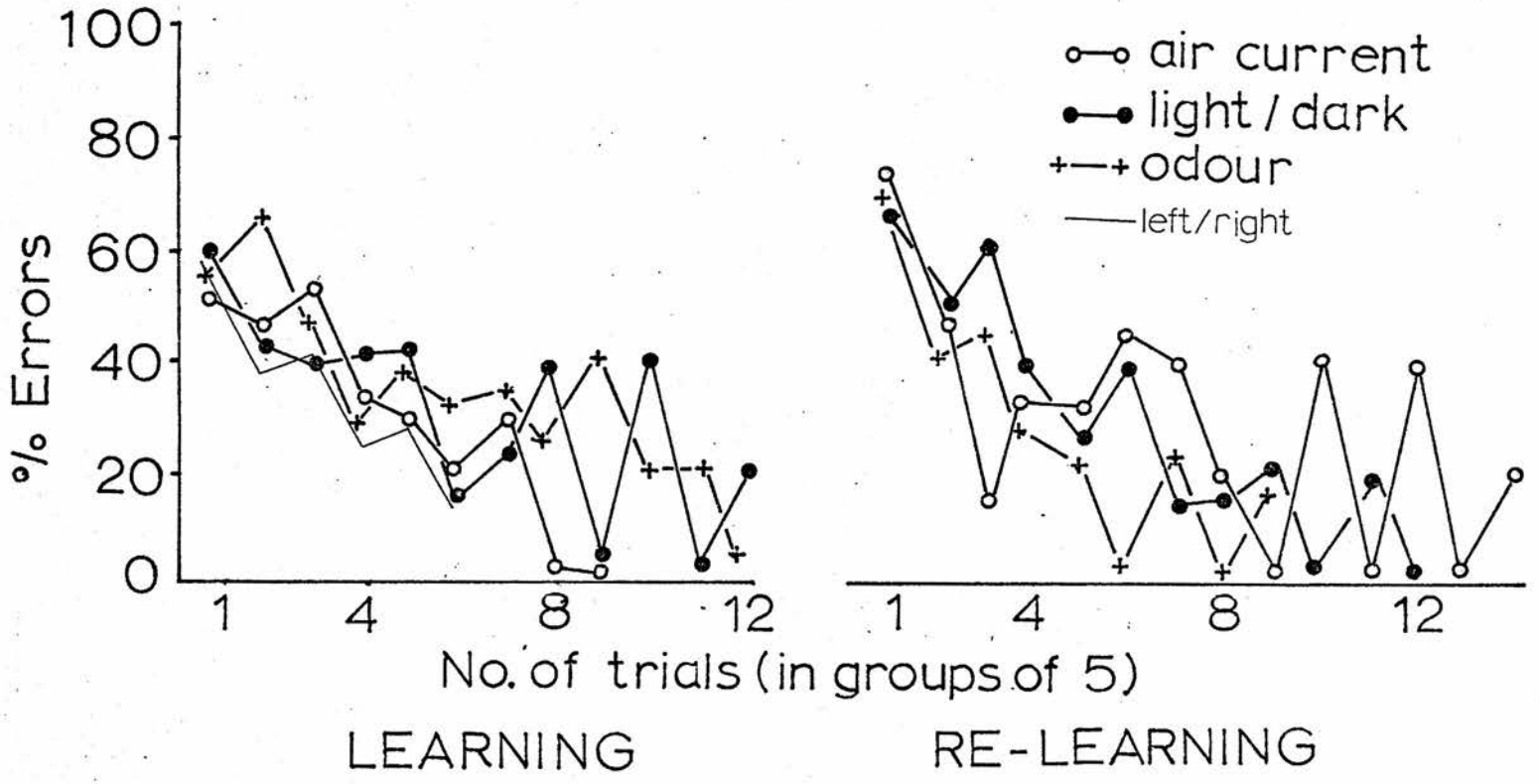
/ was varied randomly from trial to trial so that the cockroaches would not learn to respond to positional information. The animals were rewarded for correct choices by avoidance of electric shock. Training proceeded as follows.

An animal was picked up by its cotton loop and placed in the start box of the maze. It it remained in the start box for longer than thirty seconds a series of low level intermittent shocks (one every two seconds) was given until the animal began to move through the apparatus. The train of shocks was restarted every time the animal came to rest for longer than thirty seconds and stopped when the animal moved off again. If the cockroach made a correct choice it was left in the goal box for three minutes. If it made an incorrect choice it was immediately punished. As soon as its head entered the incorrect alley a single, low-level shock was given. The cockroach sometimes made an immediate correction and entered the correct alley. If it did, it was left in the goal box for three minutes but otherwise it was removed from the maze and kept in a glass vial for the same interval of time. At the end of this period the maze was wiped with alcohol and the next trial begun.

Five trials were given a day until an animal had reached a criterion of nine correct choices out of ten consecutive trials. When this cirterion was reached the significance of the stimuli was reversed on the following day. Thus, Group A animals were now rewarded for turning into the dark arm, Group B animals for turning downwing and group C animals for turning / .....

FIGURE SIXTEEN.

Learning curves for cockroaches learning to discriminate stimuli in a Y-maze.



/ turning into the odour-free arm. This reversal was carried out to ensure that any apparent learning was not in fact due to a spontaneous preference for one of the stimulus values. When animals had reached criterion again the experiment was stopped.

Results

All the animals learnt to discriminate the two stimuli they were presented with and re-learnt the discrimination when the reward was shifted to the previously negative stimulus. Learning curves for initial learning and for re-learning are plotted in figure sixteen. The results from the three groups of animals are represented by different graphs. Each curve is averaged for a group of five animals. As results are averaged from blocks of five trials each point on the graph is a mean of twenty-five separate results. Also plotted onto the graph are the results of the positional discrimination carried out under similar conditions and described in Section six. It can be seen that all these discriminations were learnt rapidly and at a similar rate.

Conclusions

In a maze situation cockroaches were able to learn to discriminate a number of stimuli. All of the stimuli appeared suitable for use in a reversal learning experiment. Light cues were eventually chosen because it is somewhat easier to control the presentation of these stimuli. A reversal learning experiment using light cues is described in the next section.

It is interesting to note that in the maze situation cockroaches / .....

/ cockroaches had no difficulty in learning to respond to specific cues and in ignoring irrelevant positional information. It was shown in the previous section that in a shuttlebox cockroaches cannot learn to ignore the place where they are shocked and respond only to a warning cue. In the shuttlebox, however, the animal is not confronted with a simultaneous choice between different stimuli as it is in the Y-maze. The situation-with-warning-cue and situation-without-warning-cue are separate successive events. In this kind of problem it appears that the cockroach cannot learn appropriate behaviour patterns for each situation. Another problem in which information is presented in a successive rather than simultaneous manner is described after the reversal learning task.

B: Multi-reversal learning

Introduction

The significance of comparative studies of multi-reversal learning has already been discussed in the general introduction. It has been claimed that four invertebrate species; Octopus, the isopod Porcellio scaber, the cockroach and the earthworm show progressive improvement over a series of discrimination reversals.

In the experiments with Octopus a very marked improvement was seen. This change in behaviour has been convincingly shown to be comparable with that seen in mammals. (Mackintosh 1962). The behaviour of Porcellio scaber also shows a highly significant change over a series of reversals. In this experiment / .....

/ experiment animals were trained to turn one way in a T-maze until they reached a criterion of nine correct choices out of ten consecutive trials. The correct turn direction was then reversed until the animals again reached criterion and so on. In the initial training series animals made an average of 27.5 errors before reaching criterion while after eight reversals they made only 8.6 errors before reaching the same criterion. It was claimed by Morrow and Smithson (1969) that this change demonstrates the formation of a learning set. However, an important control is missing from this experiment. Before it can be claimed that a learning set has been formed it is necessary to show that the improvement made by the animal is a function of reversal experience and not simply an adjustment to the experimental situation as a whole. The behaviour of a group of animals after a series of reversals must be compared with that of animals which have had equivalent experimental experience without reversal experience. In this experiment with Porcellio a group of animals should have been trained to turn one way only, for the same number of trials as received by the reversal group. At the end of this period both groups should have been given reversals. If the two groups both showed similar improvement in re-learning the discrimination it would suggest that they had improved not because of reversal experience but only through general experience of the experiment. This experience might simply be habituation to some distracting feature of the apparatus after / .....

/ after which the animal performs more efficiently on the discrimination.

This kind of explanation of improvement was proved to be the case in experiments with the earthworm (Datta 1962). Although it showed improvement over a series of reversals there was little difference in the improvement shown by a reversal group and a control group which had had equivalent experimental experience. The improvement shown by Porcellio is large but without a control experiment its significance is impossible to assess.

In the experiments described below, cockroaches were trained to criterion on a series of reversals of a visual cue and full controls were included. As well as recording changes in the number of errors to criterion with successive reversals an attempt was made to look at error patterns. These may help to tell us more of what the cockroach is actually learning about the situation. The only study to be carried out on reversal learning in the cockroach (Longo 1963) looked at a series of positional reversals. Although no improvement as a function of reversal experience was found, only ten reversals were given to a group of animals receiving forty trials on each reversal. It was hoped that training for a longer period and to a criterion of acquisition might be more successful.

Apparatus

The apparatus was identical to that used in the light/dark / .....

/ dark discrimination in section 7 of this thesis. A perspex Y-maze of the floor plan shown in figure five had its goal arms differentially illuminated and was stood upon a resistive sheet.

Subjects

Twelve adult male animals were individually marked and kept in the small culture tank. Each animal had a small cotton loop waxed to its thorax. The cockroaches were returned to the culture tank between experimental sessions.

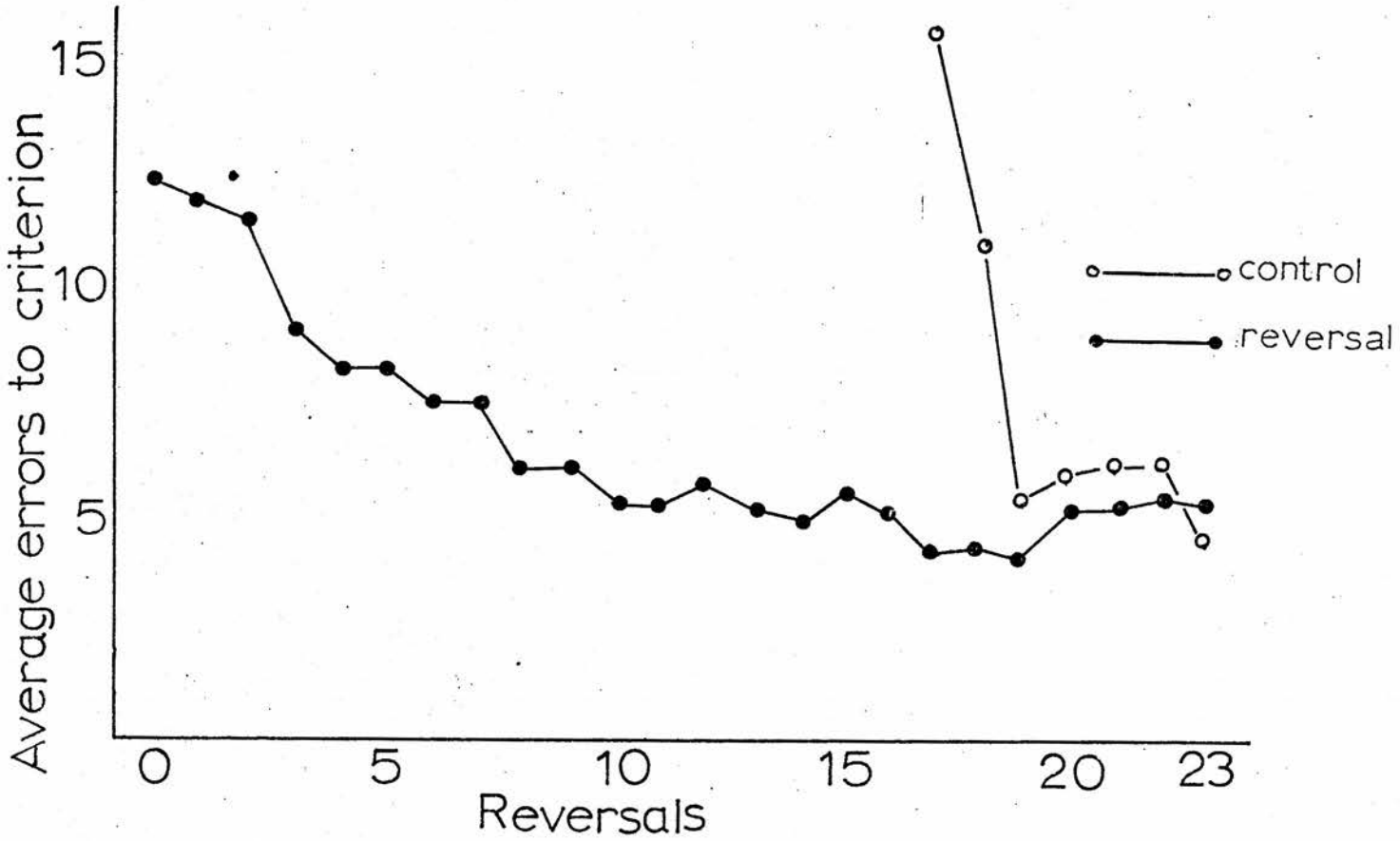
Methods

The cockroaches were divided into two groups, a reversal group and a control group. Initially, both groups received the same treatment. Each animal was placed in the start box by means of its cotton loop. If it had not started to move through the maze after thirty seconds or if at any time it halted in the maze for longer than thirty seconds then low level intermittent shock (one shock every two seconds) was given until the animal began to move. If the animal made a correct turn it was left in the goal box for three minutes. An incorrect turn was immediately punished by a single electric shock. The animal was then removed from the maze unless it had made an immediate correction. It was then kept in a glass vial for three minutes after which the apparatus was wiped with alcohol and the next trial begun.

All the animals were initially trained to turn into the lighted arm of the maze irrespective of its position which was varied from trial to trial in a random fashion. The / .....

FIGURE SEVENTEEN.

Graph showing changes in errors to criterion over a series of reversals of a visual discrimination.



/ The animals in the reversal group then had the significance of the stimuli reversed every time they reached a criterion of nine correct turns out of ten trials. The animals in the control group continued to be trained to visit the lighted arm. When the reversal group had passed through 18 reversals (after an average of 370 trials) and the control group had received an equivalent number of trials over the same period of time, both control and reversal groups were reversed every time they reached criterion. This procedure continued for six further reversals. Throughout the experiment reversals were given daily, i.e. each day each animal was trained to criterion once.

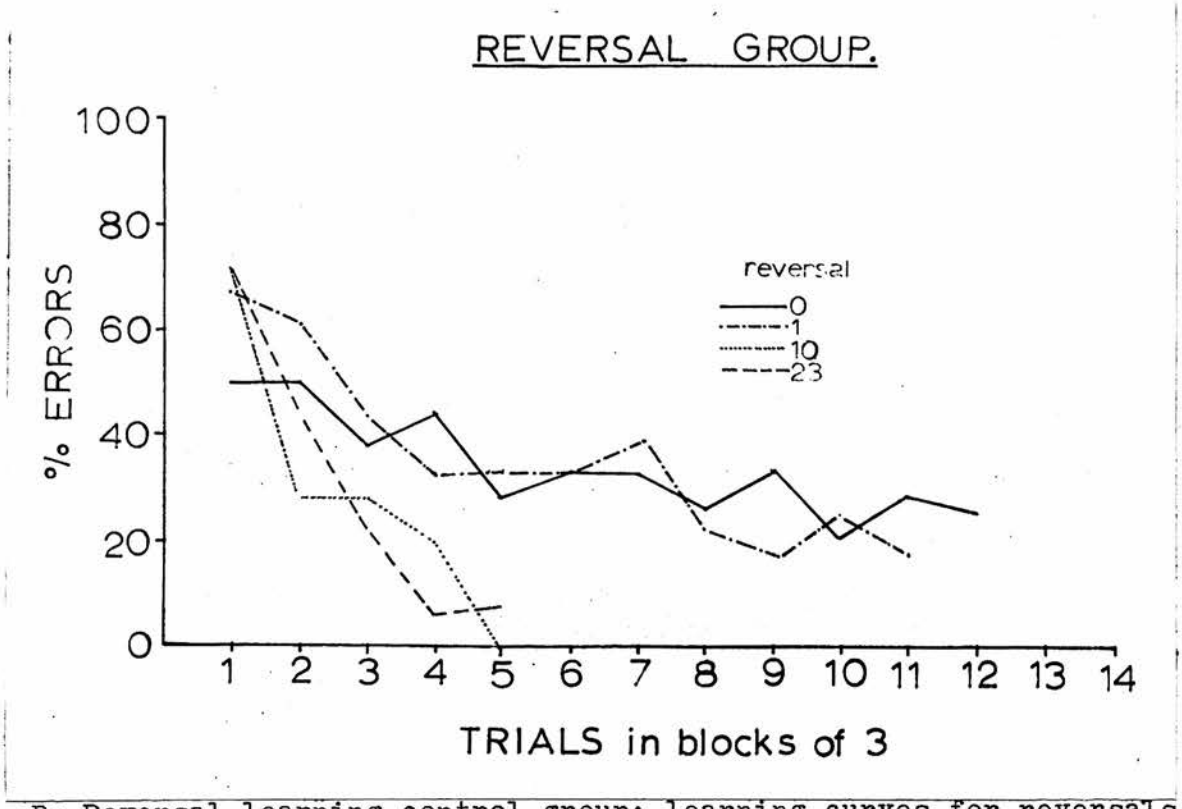
Results

The average number of errors made before reaching criterion for the twenty-three reversals of the reversal group and the six reversals of the control group are plotted in figure seventeen. Each group contained six animals so each point on these graphs represents the mean of six results. It can be seen that the reversal group showed a marked decrease in the number of errors to criterion with reversals. On first learning the discrimination (reversal 0) animals made an average of 12.2 errors before reaching criterion. By reversal twenty-three animals were making an average of only 5.1 errors to criterion. However, the control reached this same level of performance after only three reversals. This suggests that the improvement seen is not entirely a function of reversal experience. An examination of the error curves supports this view.

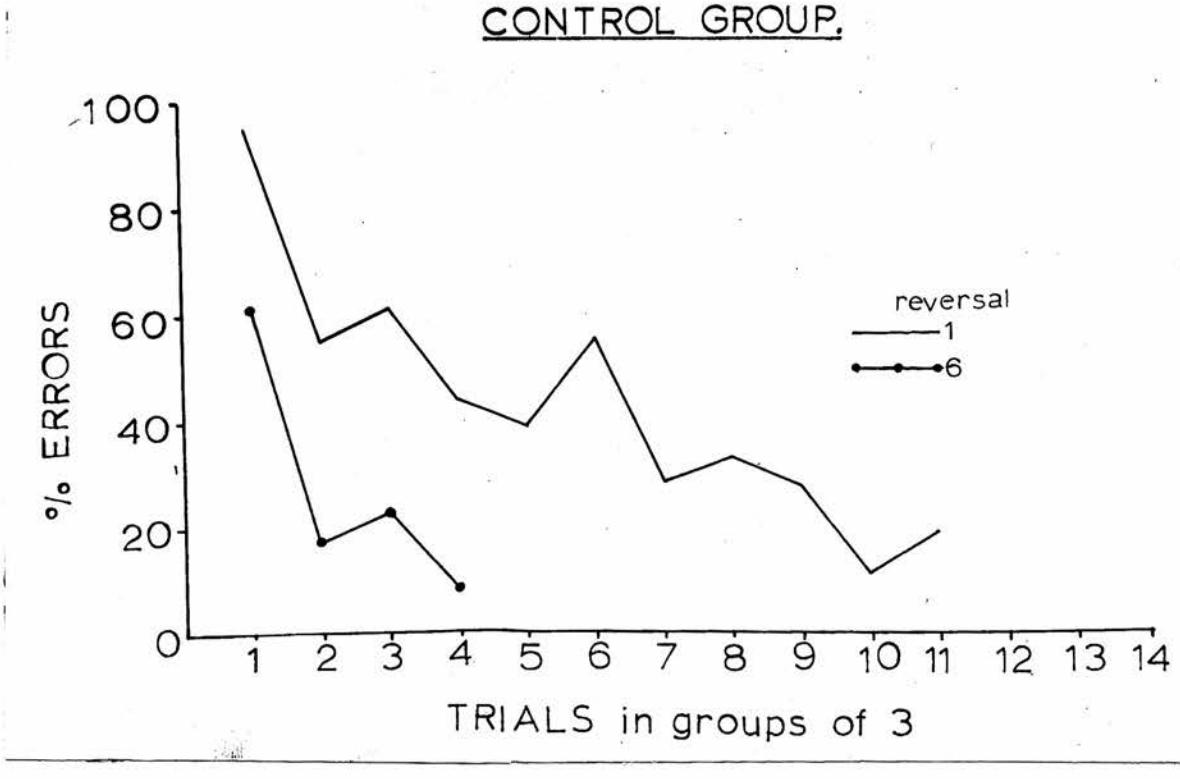
The / .....

FIGURE EIGHTEEN.

A: Reversal learning; learning curves for reversals 0, 1, 10 and 23.



B: Reversal learning control group; learning curves for reversals 1 and 6. All animals received 370 trials before the first reversal.



/ The average learning curves for reversals 0, 1, 10 and 23 of the reversal group are plotted in figure eighteen A and learning curves for reversals 1 and 6 of the control group in figure eighteen B. In each curve the percentage errors averaged for the group of six animals is plotted against trials. As trials are averaged in blocks of three each point on each curve is a mean value of eighteen results. It can be seen that in the initial learning curve of the reversal group (reversal 0) the animals begin at random choice and learned to solve the discrimination slowly. Later reversals showed much higher initial errors as the stimulus had been reversed and animals began by visiting the previously correct cue. However, the curve has a much steeper slope so the cockroaches reached criterion much more quickly. A higher initial error score is associated with a steeper gradient in the learning curve. Similarly, looking at the control groups final learning curve (reversal six) the same form is seen as in the reversal groups twenty-third reversal; an above chance initial error score is followed by a rapid decline. Also, more importantly, the first reversal of the control group shows the same steep gradient as the final reversals of both groups. The first reversal of the control group began with almost 100 per cent initial errors and thus took a larger number of trials to fall to the low value needed to achieve criterion. Although on this first reversal the control group showed a very high initial preference for the previously rewarded option, presumably because of the long training on this cue, the learning curve shows the steep gradient characteristic of late reversals and quite unlike the / .....

/ the low gradient initial curve of the reversal group (reversal 0). It is possible that if it were not for the high preference for the previously rewarded stimulus the control group would have performed as well on its first reversal as the reversal group did on its twenty-third.

It seems reasonable to conclude from the above that the changes seen in the cockroach are unlike those seen in mammals and are a function of general experience in the experimental situation rather than reversal experience or 'set-learning'. These results are further discussed after the results of the conditional reversal learning problem have been described.

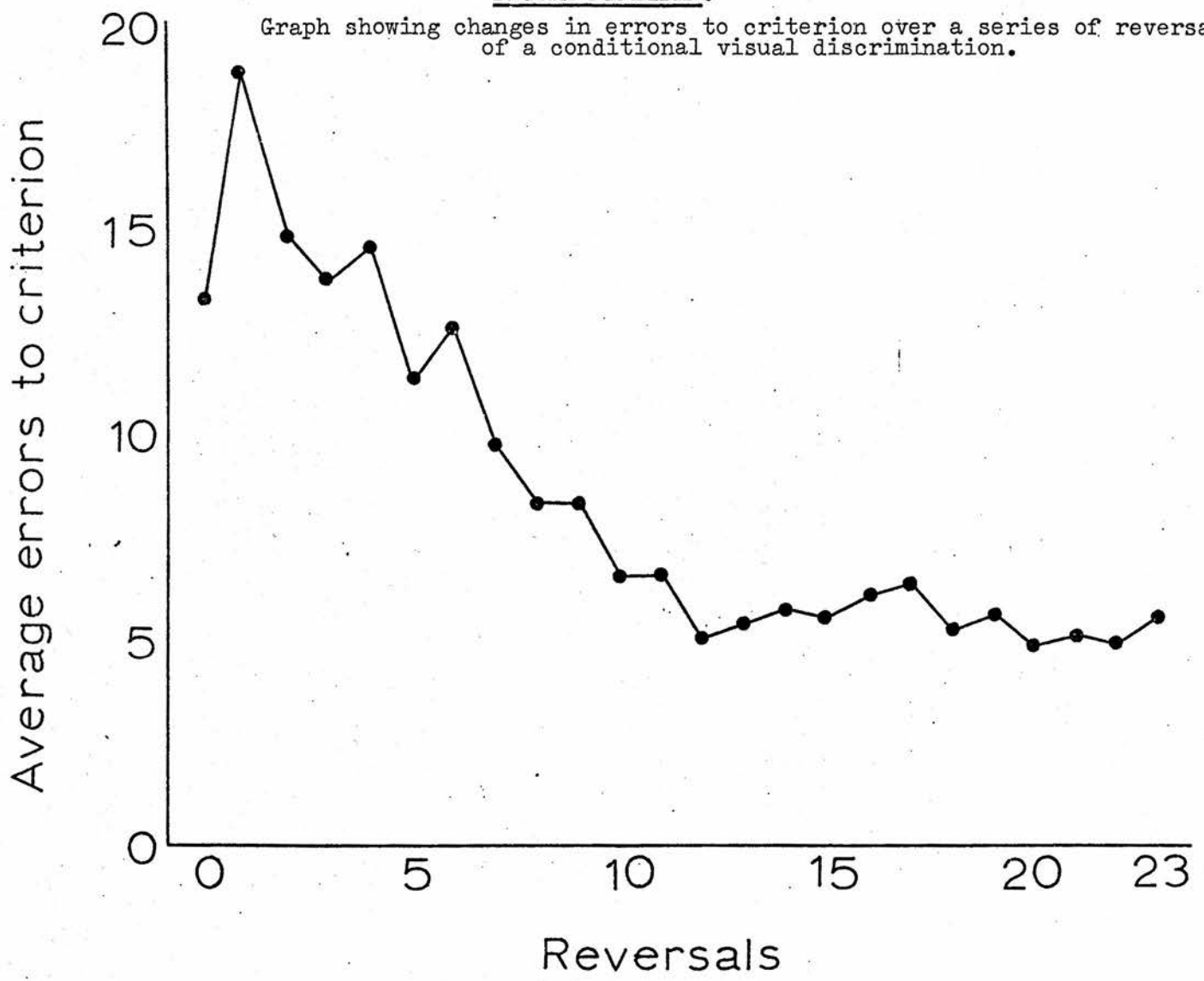
C: Conditional-reversal learning

Introduction

This experiment is identical in its form to the previous one except that an additional cue signals which of the two options is rewarded. The maze stem - the alley leading from the start box to the choice point - could be made either black or white. Whether the approach alley was black or white signalled which of the two options was correct. Whenever the correct option was reversed the colour of the maze stem was changed. This problem has features in common with the conditional problems discussed in the general introduction, the correct option is conditional upon a second cue. Also, like the shuttlebox situation, information is presented successively. The maze stem colour serves as a signal which is / .....

FIGURE NINETEEN.

Graph showing changes in errors to criterion over a series of reversals of a conditional visual discrimination.



/ is present in different forms on different trials.

Apparatus

A perspex Y-maze was used identical in its floor plan to that of the previous experiment. The maze stem was arranged so that it was detachable and either a black or a white maze stem could be put in its place. In either arrangement the two arms leading to the goals could be differentially illuminated as in the previous experiment.

Subjects

Six adult male Nauphoeta cinerea were individually marked and kept in the small culture tank. Each animal had a small cotton loop waxed to its thorax.

Methods

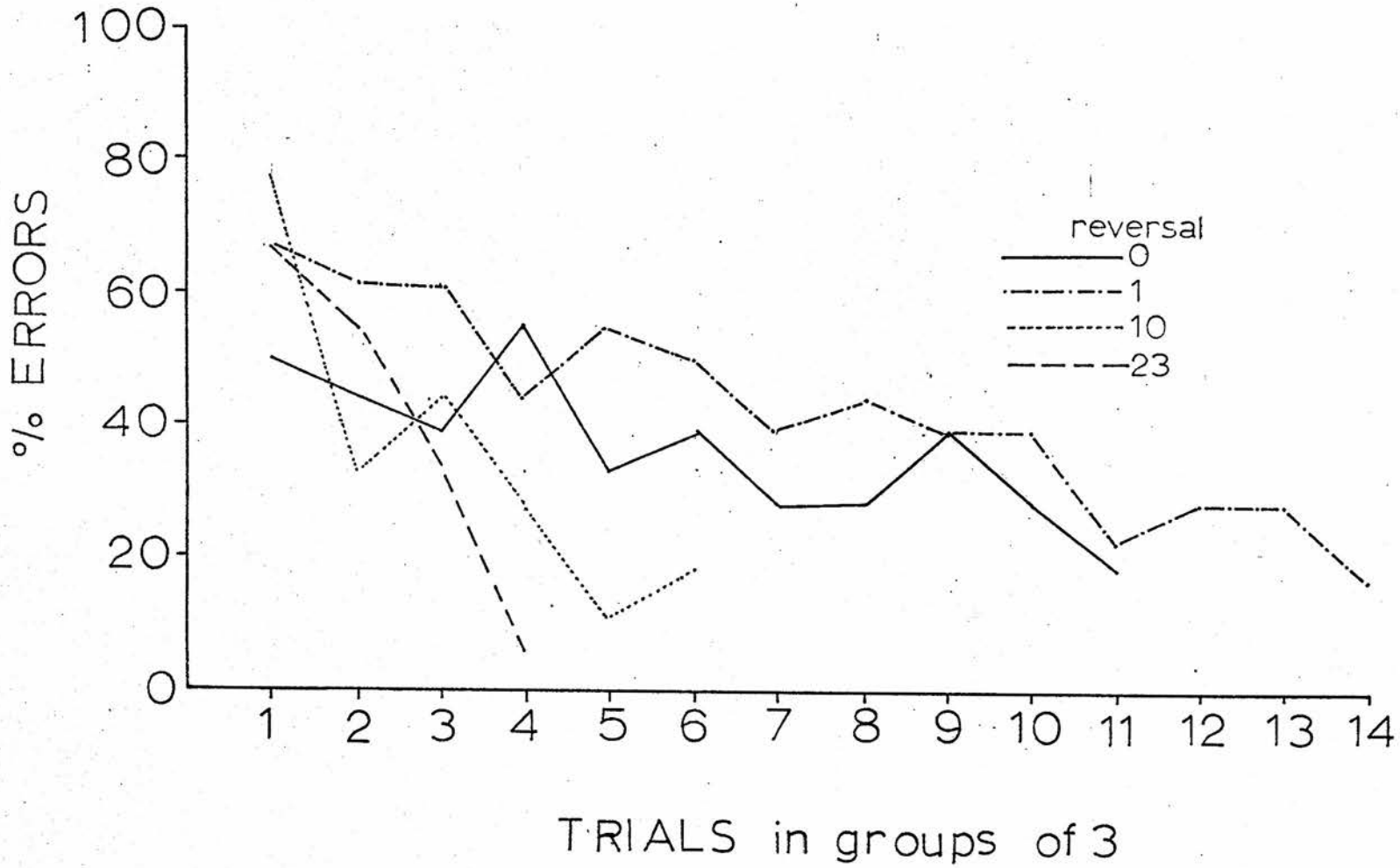
The experiment was carried out in a manner identical to that of the reversal group of the previous experiment. Cockroaches were first trained to turn towards the lighted arm irrespective of its position and when they had attained a criterion of nine correct turns out of ten trials, the correct option was reversed. However, in this experiment whenever the cockroaches were being trained to turn towards the lighted arm the white approach alley was in place and when towards the dark arm, the black alley was in place. Thus the colour of the alley leading to the choice point signalled which of the two options was correct.

Results

The average number of errors to criterion is plotted in figure nineteen . The results are averaged for the entire group / .....

FIGURE TWENTY.

Conditional reversal learning: learning curves for reversals 0, 1, 10 and 23.



/ group of six animals. If these results are compared with those of the previous reversal group and reversal control group it can be seen that although the form of the curve is different by their final reversal all the groups reached the same level of performance. The addition of an extra cue in no way helped the animal to improve over a series of reversals. Once again the animals did not reach a level of performance superior to that reached by a control group after only three reversals. Thus in both the reversal learning problem and the conditional reversal learning problem the only improvement over a series of reversals appears due to general adaptation to the conditions of the experiment. This point of view is supported by the form of the curve seen in figure twenty-one. On the first reversal the conditional animals show a marked increase in the number of errors to criterion followed by a gradual improvement over further reversals eventually reaching the same level of performance as the reversal group. It seems probable that the change in the maze from a black stem to a white stem slows down the process by which the cockroach gets used to the experimental situation.

Learning curves for conditional reversals 0, 1, 10 and 23 are plotted in figure twenty-[illegible]. It can be seen that the gradient of the reversal 1 curve is the same as the original learning curve but as the animals begin with a higher number of initial errors they take longer to reach criterion. Gradually, however, the animals show the same steepening of the graph as the simple reversal groups and by reversal ten both groups show curves very similar in their gradients / .....

/ gradients and in their initial errors.

Conclusions

Although the cockroach does not learn to use the extra cue as a signal, the results of this experiment confirm the conclusions drawn from the previous one. The imporvement in rate of learning with reversals is due to general experimental improvement, but this process is slowed down when the apparatus changes between reversals. It is difficult to know what phenomena underly this very striking improvement in performance. Possibly, part of it is due to the inhibition of competing responses such as attempts to climb the walls (which are too low for the animal to successfully avoid shock) and time spent investigating cracks between the walls and the floor of ceiling. If the animal behaves in this way near the choice point it may choose more randomly than after it has habituated to these distractions. Part of the change appears to be due to the animal learning its way around the maze. In the early trials it is common to observe that the animal remains stationary in the start box or the approach alley of the maze. When the shock comes on the animal then runs in a wild 'panic'. When the animal has had some experience of the apparatus it behaves quite differently. When placed in the goal box it generally sets off at a steady trot, slows down at the choice point and makes a gradual, hesitant advance followed by cessation of movement or punishment. More and more frequently with experience it makes an immediate correction when punished. However, these changes in behaviour are rather obvious and take place quickly. No behavioural / .....

/ behavioural change was observed which correlated with the long term changes in speed of reversal learning. Little is known about the changes which might underly this sustained improvement in performance, for although the cockroach does not show 'true' reversal learning improvement it does show a large and adaptive improvement in its ability to avoid punishment and solve this mzae problem.

The inability of the cockroach to improve over a series of reversals as a function of reversal experience fits in with the general pattern of comparative data described in the general introduction. The cockroach as a 'lower' animal shows a pattern of behaviour similar to that seen in the earthworm, fish and crab. It is interesting to note that in some experiments (Wodinsky and Bitterman 1957) in which the fish was found to improve over a series of reversals all the improvement could be accounted for in terms of experimental experience as could the results reported here. Improvement is not generally seen in fish because extensive pre-training is usually given during which the subjects become accustomed to the experimental situation. In the experiment with fish in which improvement was seen a set of learning curves was produced which were progressively steeper in slope but which showed increasingly higher numbers of initial errors, just as found in the cockroach experiments. In rats and pigeons recovery from this transfer of information from the previous reversal occurs and the animals eventually show a decrease in initial errors. As described in the general introduction, Bitterman and his colleagues have attributed this fall in initial errors to proactive inhibition. They suggest the animal finds it increasingly hard / .....

/ hard to remember which option was last rewarded and at the start of a new reversal tend to behave more randomly. It is possible, at least in part, that the behaviour of the cockroach differs from that of higher animals because of what has been called 'an inability to forget' (Gonzalez and Bitterman 1967).

11.

LEARNING IN A SEMI-NATURAL SITUATION.

Introduction

The previous experiments have studied the behaviour of the cockroach in situations similar to those used in the study of learning in higher organisms. These studies have demonstrated learning in a number of avoidance situations and have suggested the possible limits of the cockroach's learning ability. Although the apparatus and techniques were designed to suit the cockroach' particular sensory, motor and motivational systems they may not be adapted to display the cockroach's learning ability. In this section avoidance learning in a semi-natural situation is studied and attempts are made to relate the results to the previous 'laboratory' studies on avoidance learning.

Male Nauphoeta cinerea were kept in large tanks containing perspex sheets, glass vials and wooden blocks which provided a diverse environment full of nooks and crannies (see figures twenty-one and twenty-two). This arrangement was modelled upon the apparatus developed by Ewing (1970) in her extensive studies of the social life of this cockroach. She has shown that in this situation cockroaches develop a hierarchical/ territorial society. The following description is drawn from her work.

Once a group of males has become established in a tank they can be divided, for the purposes of description, into three categories based on dominance. The most dominant or alpha animals / .....

animals occupy and defend areas within the tank. They spend nearly all their time on their territories and patrol up and down them attacking and driving away intruders. Alpha animals rarely encounter one another as they generally remain on their territories but they will win fights against all other animals wherever they may occur in the tank. Generally, when a fight does occur the alpha-male rushes at the other animal which flees before any physical contact is made.

Beta males occupy small sites and will defend them against other animals. Although easily driven from these sites by alpha animals they can defend them successfully against other beta and gamma males. Betas patrol only small areas and avoid other animals they meet in the open.

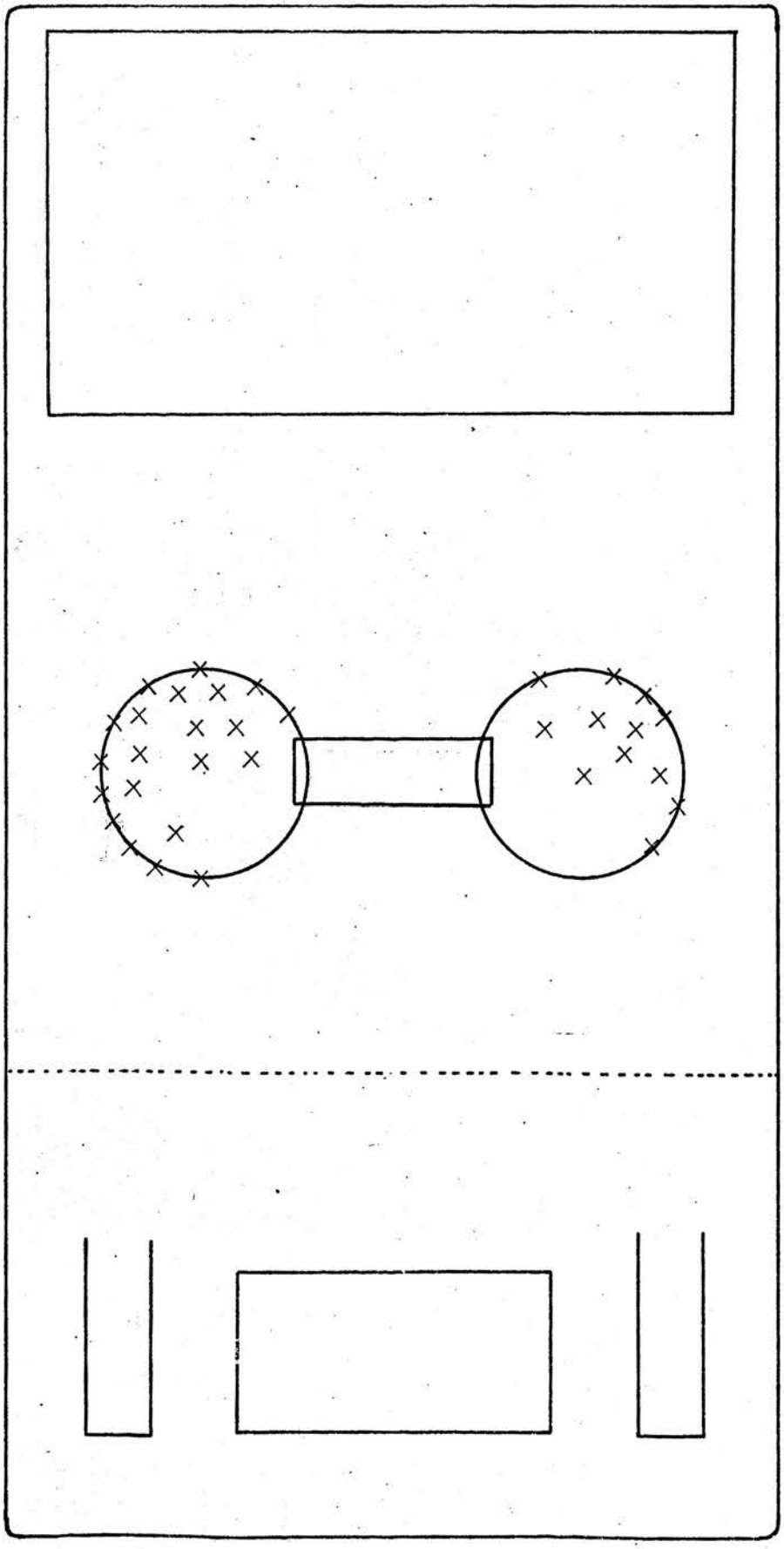
The lowest ranking or gamma males are submissive animals which rarely occupy even a small area for more than a few days. These animals are only occasionally seen to fight but spend much of their time making non-aggressive attempts to enter other cockroaches territories.

Dominance and territory possession are linked in the cockroach. Only the most dominant animals will hold large territories and patrol around them while the least dominant animals will hold no territory at all. The hierarchy is not fixed and any animal may move up or down the range, even a gamma animal may move up the hierarchy and eventually drive out an alpha and take over his territory.

When a fight does occur a fairly consistent pattern of events is observed, although how far the fight goes will depend / .....

FIGURE TWENTY-ONE.

Plan of Cockroach Tank



x-spontaneous flight

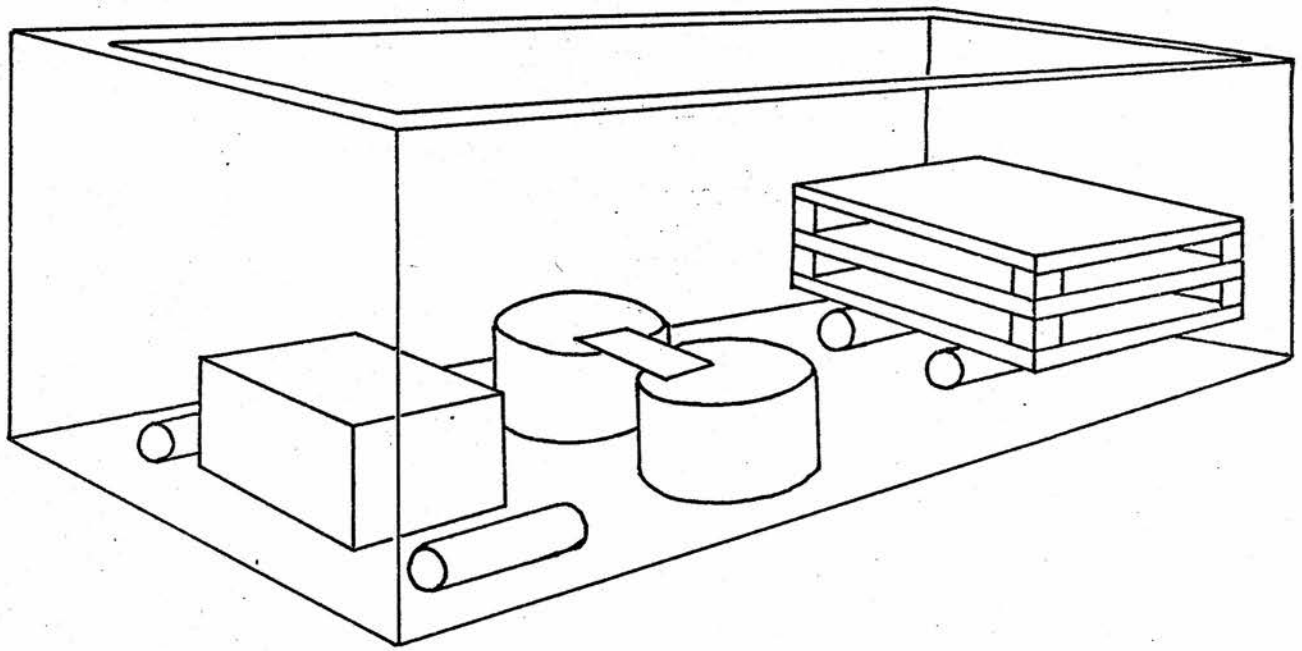
/ depend upon how well matched and how dominant the animals are. Before fighting begins two animals assume aggressive postures. They face one another with their abdomens fully extended and arched upwards and their legs stretched so that their bodies are carried well off the ground. They may lash at one another with their antennae and then charge and butt their heads together. If one animal can get its head under its opponent's body it may toss the other animal onto its back. In severe fights animals may grapple with their legs locked together and bite at each other as they roll over and over.

The initial aggressive posture or a sudden rush by one animal may be sufficient to persuade the other to run away. If not, one animal usually emerges superior within a few minutes. The loser flees and if chased by the victor shows a characteristic submissive posture. It lies still and tucks its limbs under its body and its head under the shield of its pronotum. The body of the animal is pressed close to the ground and its antennae lie flat. The winner may then stand upon the back of the submissive animal but usually ceases to attack it.

When animals are first put into a tank there is a great deal of fighting but soon a fairly stable hierarchy is established. One of the most striking changes in behaviour observed is the establishment of large territories by the alpha males and the subsequent avoidance of these areas by the subordinate animals. In the tank used in these experiments, shown / .....

FIGURE TWENTY-TWO.

COCKROACH TANK



/ shown in figure twenty-two and in plan in figure twenty-one, it was found that the central area consisting of two glass dishes containing food and water and the bridge between them was always occupied as a territory by the top alpha male in the tank. This area seemed to be highly preferred, perhaps because it contained the only food and water supply in the tank and had clear boundaries at the dish/floor interface. The alpha male occupying this territory was always very noticeable. It patrolled around the area, rarely descending to the ground, with its legs maximally extended and its abdomen arched upwards as in the aggressive posture. If other animals entered the area it rushed at them and fought with them if they did not immediately flee. Other animals occupied a variety of sites in the tank, beta animals frequently occupying one of the glass vials and a small semi-circle around its mouth. Sometimes a second alpha male was seen occupying the wooden block, although this territory was never as consistently inhabited as was the central dishes and bridge area. Several animals never consistently occupied any sites.

In the experiments to follow the acquisition of the central territory area and its subsequent avoidance by other animals was studied.

Apparatus

Two identical glass tanks were set up in the manner shown in figures twenty-one and twenty-two. The tanks were 60 cm long, 30 cm wide and 30 cm high. Referring to figure twenty-two, at the near end (bottom of plan figure twenty-one) was a wooden / .....

/ wooden block (12 x 6 cm) flanked by two open glass vials (7.8 x 2.5 cm). In the middle of the tank were two glass crystallising dishes (8 cm diameter, 5 cm high), one containing rat cake and the other containing cotton wool saturated with water. The two dishes were bridged by a glass microscope slide. At the far end of the tank, three tiers of perspex sheet (28 x 16 cms) sat upon another pair of glass vials. Sawdust covered the near end of the tank floor for a distance of twenty centimetres.

The two tanks were kept under identical conditions in a light and temperature controlled room. For twelve hours of the day the room was brightly lit by neon strip lights and for the other half of the day by three ten-watt red bulbs. All observations took place during the dark phase of the cycle.

Subjects

Twenty adult male Nauphoeta cinerea were collected from a large culture tank shortly after completing their adult moult and individually isolated in glass crystallising dishes containing a food and water supply. Each animal was marked with a distinctive symbol on its pronotum with white paint. After they had been isolated for one week the animals were divided into two groups each of ten animals. At the beginning of the light phase of the daily cycle a group of animals was placed in each of the tanks.

Methods

The observations made were designed to give a quantitative / .....

/ quantitative measure of the establishment of territories and there avoidance by other animals.

The cockroaches showed a peak of activity shortly after the bright lights go off. Animals were observed daily for a period of one hour from the time of dark onset. The first observation period occurred twelve hours after the cockroaches had been placed in the tank and observations continued for thirty-seven daily periods. On three of these days experimental manipulations were carried out prior to the observation period. On days 10, 19 and 28 the alpha-male occupying the central territory area was permanently removed twelve hours before the commencement of observations. Each time a dominant is removed a new alpha-male eventually emerges to take his place. On days 10 and 28, but not on day 19, when the dominant was removed, the food and water dishes and the bridge which had comprised the territory of the dominant were removed and replaced with clean ones. The area surrounding the territory was then scrubbed successively with soap and water, water and alcohol. On day 28 in one of the tanks (tank II) the dominant was not permanently removed but was replaced after 24 hours. Several scores of behaviour were taken, these were identical for each of the two groups of animals.

1) Initially, a perspex grid marked out in one inch squares was placed on the tank. At three minute intervals the position of each individual on this grid was recorded. After a short while it became obvious that the central dishes and bridge area were always going to be occupied as a territory. / .....

/ territory. From then on only whether each individual was in or out of this area was recorded.

2) All occasions on which one animal chased another away or one animal fought another were recorded along with the identity of the individuals concerned and the eventual victor. 'Chased away' meant that one animal rushed at another which fled without any physical contact occurring. 'Fought' implied any stage in the fighting sequence described above other than simply chasing away.

3) Sometimes an animal would be seen to flee spontaneously without any attack occurring. If an animal showed a sudden change of direction and ran without any noticeable stimulus then 'spontaneous flight' was recorded. The position from which the animal fled was noted.

Results

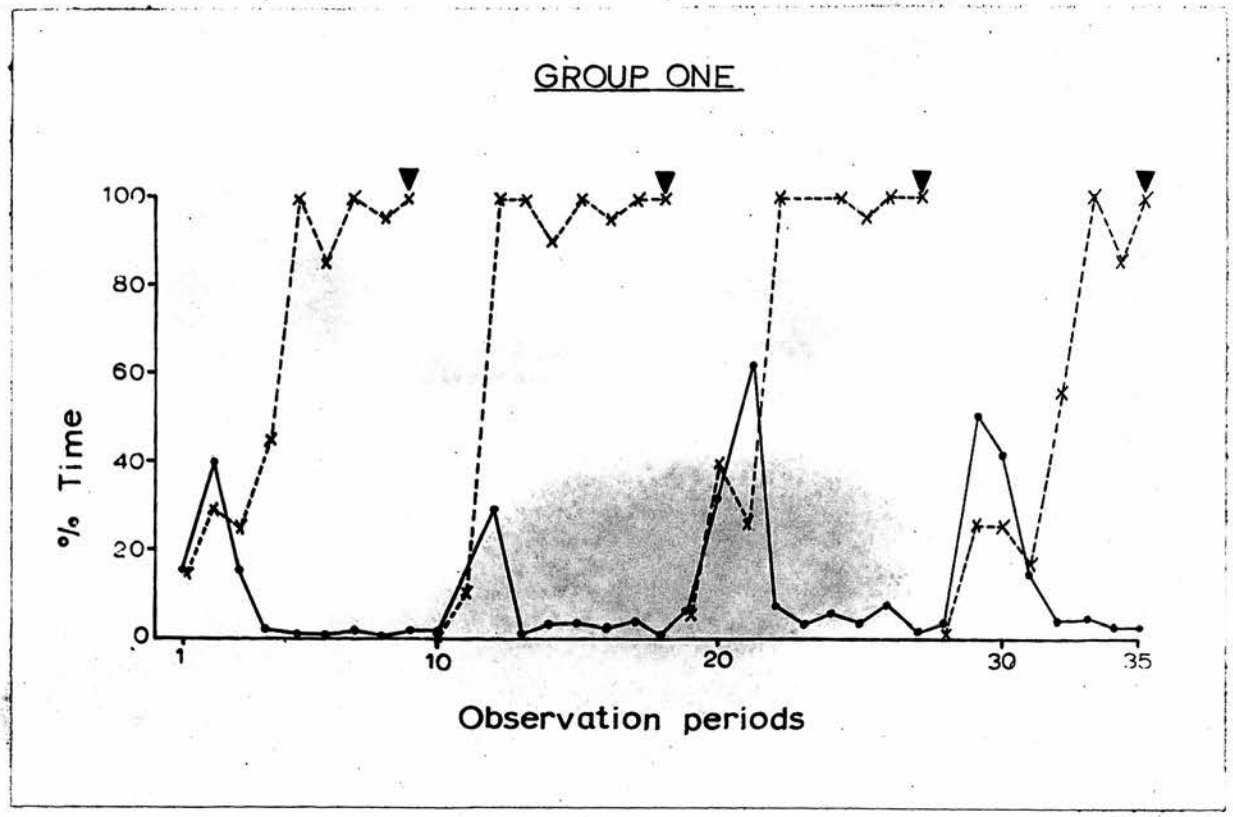
The position of animals had been recorded every three minutes during each hourly observation period. From this measure was calculated the percentage time in each hourly observation period, spent in the central territory area by the dominant animal and by the subordinate animals. As mentioned above the alpha male occupying the central territory area is easily identified in a number of ways. As continuous records of all the animals had been kept it is possible to trace the behaviour of the dominant separately both while he is occupying the territory and in the time before he established dominance. In this way we can examine changes occuring during the emergence of territory possession.

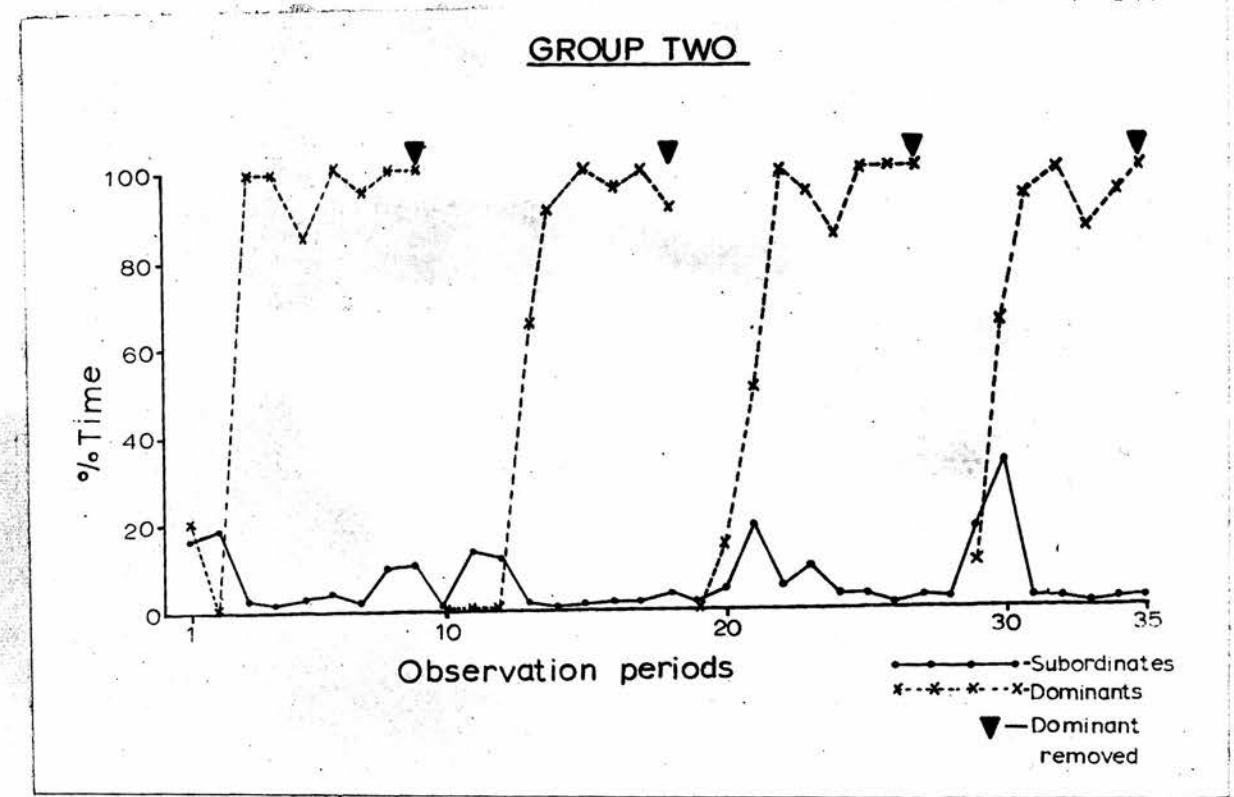
These / .....

FIGURE TWENTY-THREE.

Graphs showing the acquisition of territory by cockroaches.

The curves show the percentage time spent in the territory area plotted against observation periods. The dotted line is for the dominant animal and the full line for the group of subordinates. The dominant was removed on periods 10, 19 and 28.





/ These results are plotted for each tank in figure twenty-three. The percentage time spent in the central territory area is drawn against observation periods for the dominant and the subordinates. The graph for the dominant animal is shown as a dotted line, each point on it represents the percentage time spent in the central territory area (i.e. the area comprising the two dishes and bridge) during a particular observation period. The graph for the subordinates is shown as a full line, each point on it represents the percentage spent in the central territory averaged for all the subordinate animals for a particular observation period. Tables will be found in the Appendix 9 which show all the fights involving the dominant animal, classified according to whether he won, lost or merely chased the other animal away without fighting. Although the two tanks showed different levels of fighting and activity similar patterns of changes with time were observed.

Initially, both the dominant animal (or rather the animal that is about to become dominant) and the subordinates spent about the same amount of time in the central territory. Over the first few days a large number of fights occurred. Gradually, the dominant established his territory and spent more and more time on it while the others spent less and less time there. By day three (tank 1) or day five (tank 2) the dominant had firmly established himself, spending almost a hundred per cent of his time on his territory and being involved in a few fights. Most of the encounters that did occur consisted of the dominant chasing other animals out of the central area. By the same period the percentage time spent / .....

/ spent in this area by the subordinate animals had fallen almost to zero. Animals still occasionally tried to enter the territory, perhaps because it contained the only food and water supply.

During the next phase of the experiment, the dominant animal was removed and the territory cleaned and glassware replaced. At first the subordinate animals hardly ever entered the territory area even though there was no longer any risk of them being attacked nor any odour cues remaining from the previous occupant. Only by the second or third day after the removal of the dominant did animals once more begin to enter the territory. Soon they began to spend a large amount of their time there and fighting became more common again although it did not reach the levels observed when animals were first introduced into the tank. Shortly after this a new dominant emerged, won fights against the other animals and was soon spending all his time in the territory while again the other animals are rarely seen there.

This pattern of changes was seen every time the dominant is removed whether or not the area was cleaned and dishes changed (compare changes after days 10 and 28 with 19). After a delay animals moved into the territory area more fighting occurred and a new dominant emerged and drove away the subordinate animals. The exact time course was seen to vary from removal to removal. In tank 1, on day 28 when the dominant was removed, it took some six days before the new alpha male established himself, possibly because all the most dominant animals had already been removed.

This / .....

/ This set of results strongly suggests that avoidance of the territory of the dominant is a learnt phenomenon. It is clearly not dependent upon odour or other markings as cleaning the area has no effect upon the time course of events. Rather it appears that animals learn to avoid the territory as a result of being attacked there and this behaviour extinguishes when the alpha is removed.

Spontaneous flight scores support this view. The places where this behaviour was observed are plotted onto the plan of the cockroach tank in figure twenty-one. It can be seen that this behaviour occurred only in the area of the tank which constituted the territory of the alpha male. Flight occurred as frequently during the observation period immediately after the dominant was removed (four times in six days) as on days when there was a dominant present (26 times in 43 days). However, although this behaviour pattern was seen on the day immediately after dominant removal, it was not seen at all on the two days following this during which a new alpha male was establishing himself (see Appendix 9). It seems that this behaviour is rather similar to the spontaneous crossing seen in the shuttlebox. The animal has been punished in a particular area and develops a 'fear' of it which causes it to flee without actually being attacked. When the dominant is removed this 'fear' gradually disappears and spontaneous runs stop until a new dominant emerges. It is interesting to note that, just as in the shuttlebox situation, the animal although having learnt to avoid a particular place and showing spontaneous runs from it does not learn the exact cue which it should be avoiding. This cue is the dominant animal or the / .....

/ the dominant-upon-territory rather than the territory itself. Animals do not learn that it is safe to enter the territory when the dominant is temporarily away although not safe when he is there patrolling about.

In the final part of the experiment with tank two the dominant was not permanently removed but replaced after twenty-four hours. Despite this period away from the tank the animal managed to regain its position of dominance by the third day.

Conclusions

Subordinate cockroaches learn to avoid the territory of dominant animals. When the dominant is removed animals are no longer attacked in this area and the avoidance extinguishes. A new dominant animal emerges and drives other animals from the territory and the cycle is repeated. Occasionally cockroaches run from the territory without actually being attacked. They do not learn that it is only dangerous in the territory when the dominant is present. These results closely parallel previous results in this thesis on avoidance learning in a simple situation and in the shuttlebox. Once more the cockroach is demonstrated to have a remarkable ability to learn to avoid particular cues which are never present without positional cues. In this instance work from two different approaches seems to give results which are in close agreement.

A final point which merits mention is that the alpha animals / .....

animals always established their territories in the same place, the two dishes and the bridge. It may be that cockroaches have an inbuilt model of 'a good territory' which perhaps contains such features as food, water, a place to hide in, good boundary features to clearly mark its limits. Experiments which offered cockroaches a range of territories and examined the features of preferred ones would probably yield very interesting results.

EXPERIMENTS WITH THE HONEY-BEE

APIS MELLIFICA.

GENERAL METHODS.

The bees used in this series of experiments were of the original English variety, Apis mellifica mellifica. They were kept in a small, glass-sided, observation hive, this contained only two frames but supplied ample numbers of animals for the experiments. The hive was kept indoors but was arranged so that it was connected via a short passageway to an entrance and alighting board outside the building. Thus the bees were able to forage on flower beds and gather nectar and pollen as normal.

All the experiments were performed indoors in a laboratory about forty metres from the hive entrance. Bees were trained to fly into this room through an open window. This training proceeds as follows.

Firstly, a 'feeder' containing two molar sucrose was placed very close to the hive entrance. The feeder consisted of a 'Kilner' jar full of the sugar solution inverted over a glass petri dish. Between the petri dish and the rim of the jar was a disk of filter paper in which radial cuts had been made. These cuts allowed bees to suck the sugar water out through the crack between the petri dish and the kilner jar. They could also suck sugar water from the filter paper when there was not enough room for all of them to gather around the cracks.

The presence of this large flow of rich sugar solution

was / .....

/ was soon discovered and once signalled to other members of the hive caused recruitment of a large number of bees. The only time it would not work is in Spring when the natural nectar flow is so good that the bees will prefer to visit flowers. In 1971 hardly any bees would come to this feeder throughout the month of May.

When a large number of bees have become used to feeding at the dish it was moved, a few feet at a time at first, then up to ten feet at a time towards the window of the laboratory. As the window of this room lies on the first floor the final section of the journey had to be completed by placing the feeder on a tray and hauling it up on a rope. When the feeder had reached window level it was placed on the window sill a few feet to one side of the window. The bees were then allowed to settle down to feeding at this spot. Next, the concentration of sucrose in the feeder was lowered to one molar. A few bees usually ceased visiting the dish, the number depending upon the abundance of other food supplies, but usually a large number continued their visits. When the bees had once more settled down they were blown off the feeder and it was removed. At the same time the window alongside the feeder was opened wide and a dish containing two molar sucrose was put out on a table inside the room. Bees arriving to feed as usual now found the feeder gone and began to circle around the surrounding area as though looking for the missing feeding dish. A few wandered into the / .....

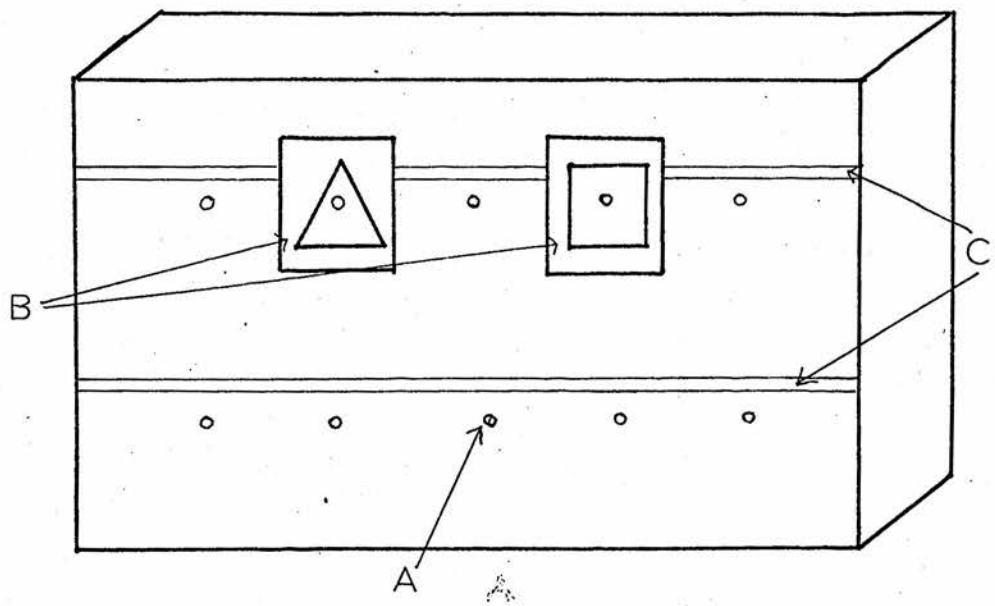
/ the room and found the two molar sucrose. As they fed, these bees were marked with a dab of paint on their thoraxes, if it was necessary to recognise individual bees a code of dabs of different coloured paints was used. The bee was usually so engrossed in sucking the sugar water that it was not disturbed by this process. When enough bees for whatever experiment was planned had visited the dish, the feeder containing one molar sucrose was replaced on the window sill. The bees that had found the two molar solution inside remained faithful to it as it was a much richer source of sugar. The rest of the bees returned to the feeder of one molar, this reservoir of bees just outside the room could be drawn upon whenever required by repeating the above procedure. Unmarked bees sometimes found the sugar solution inside the room and thus unofficially joined in experiments. Such bees were killed by striking them with a roll of newspaper.

The marked bees that were visiting the room to feed were now made to solve discrimination tasks for their sugar reward. The experiments all used visual stimuli and these were displayed in either the horizontal or the vertical plane. In both cases the stimuli were drawn on standard sized rectangles of cardboard of dimensions 10.75 to 12.25 cms.

When discrimination experiments were performed in the horizontal plane the cards were laid flat on a black table and / .....

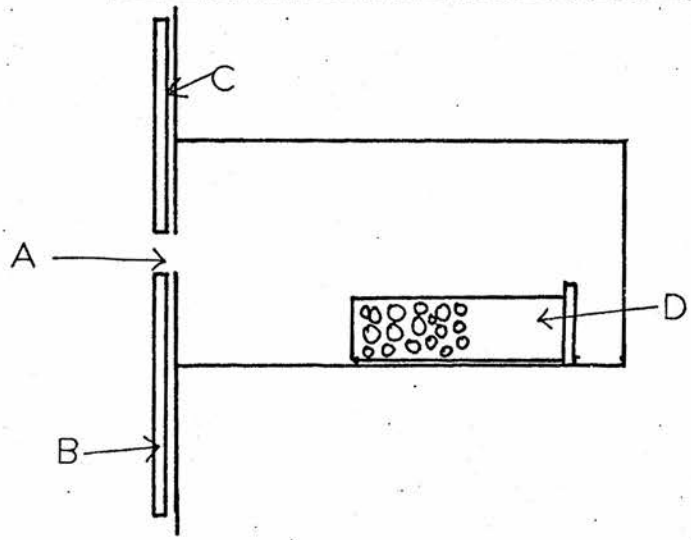
FIGURE TWENTY-FOUR.

TRAINING APPARATUS.



The apparatus was 70 x 44 cms.

FEEDING COMPARTMENT.



The compartment was tubular, 8 cms long and 5 cms in diameter

A - entrance hole
B - stimulus card
C - Velcro strip
D - feeding vial

/ and covered with a sheet of glass. On top of the glass sheet above the stimuli were placed clear plastic dishes 5.5 cms. in diameter. These contained either two molar sucrose as a reward for correct stimuli or water for unrewarded stimuli.

To display stimulus cards in the vertical plane a special apparatus was used and is shown in figure 24. It consisted of a vertical board with a set of holes in it, each hole leading into a small chamber at the back of the board. In this chamber there was a feeding vial; this was a plastic vial packed with cotton wool and with many holes pierced in its sides. The cotton wool was soaked in two molar sucrose or water, bees could feed from the vials by poking their probosces through the holes into the saturated cotton wool.

Stimulus cards were attached to the front of the apparatus by means of 'Velcro' strip, each card had a piece of Velcro on its back and the front of the apparatus had two long strips. Each card also had a hole cut in its centre, when the cards are attached to the apparatus the bees could fly up to a stimulus card, alight, crawl through the hole in its centre, through the board and into the chamber at the back where they could feed from the vials.

A transparent perspex sheet was fitted to the front of the apparatus to protect the stimulus cards. Using the apparatus shown it was possible to display up to ten cards at a time.

If / .....

If at any stage during the experiment it was necessary to adjust the apparatus, refill the vials or dishes, change the positions of the cards, clean the glass or perspex coverings etc. the inflow of bees could be stopped by closing the window. The window was hinged at its centre and swung around a horizontal axis, it is was closed so that there was a crack about an inch wide open along the botton edge bees could still get out of the room. When they flew out towards the light they hit the glass and then dropped down and passed through the open crack. Incoming bees do not find this narrow opening so no bees would enter while adjustment of the apparatus was in progress.

At all times the apparatus and stimuli were lit by light coming through the window, no artificial light was used in any of the experiments.

13.

PRELIMINARY EXPERIMENTS.

Introduction

Two preliminary experiments were carried out to design training and scoring techniques suitable for further experiments. Groups of bees were trained to discriminate a yellow card from a blue one, a task which it is well known they can accomplish easily.

Experiment one

Materials

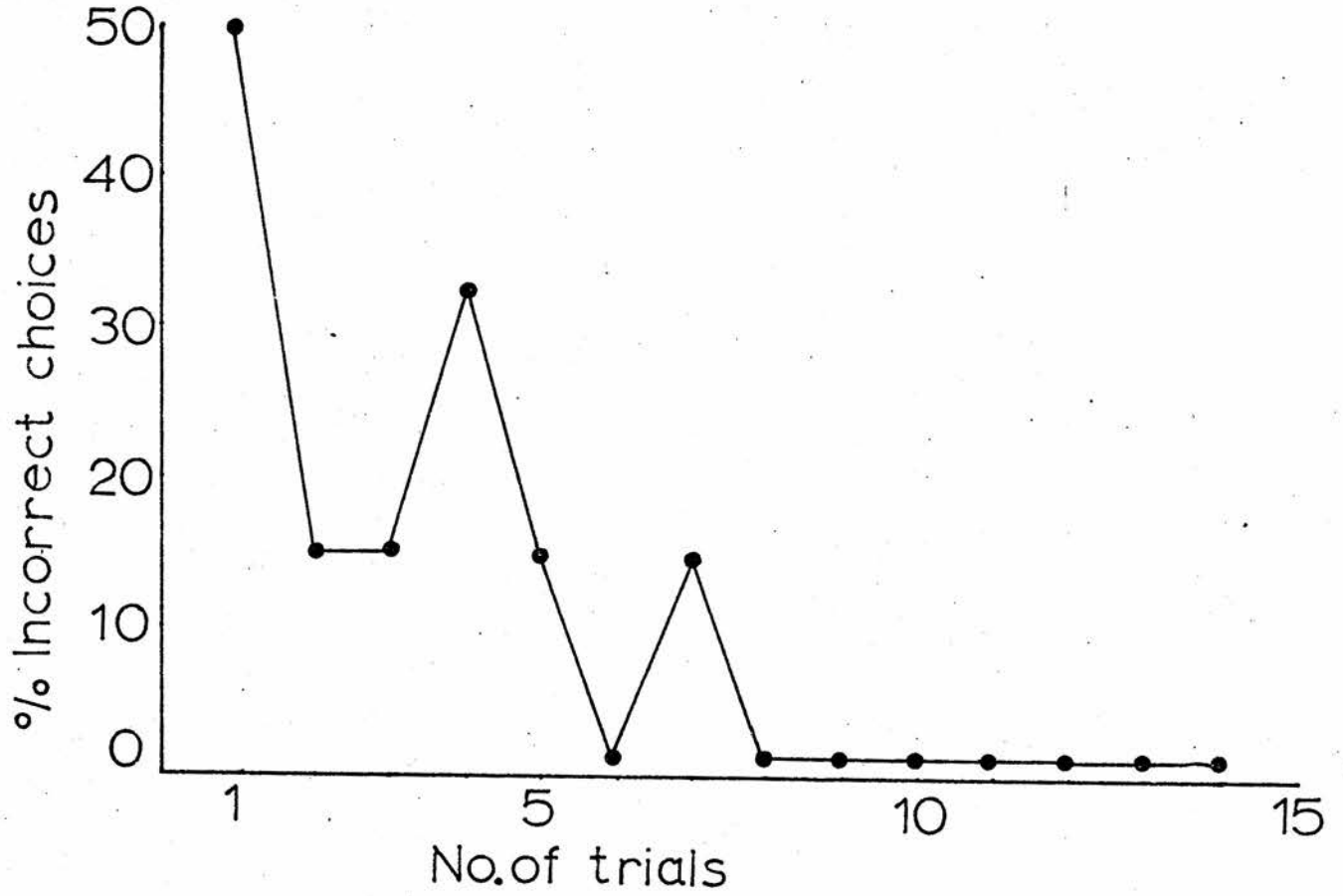
The cards were rectangular ones of the standard dimensions which had been painted with oil paints. They almost certainly differed in their brightness as well as their colour but in this experiment it was merely required that they be easily discriminable stimuli.

The experiment was carried out with the stimuli in the horizontal plane. The two cards were placed flat on the table, under a sheet of glass and one of them rewarded with two molar sucrose.

Methods

Six individually marked bees were allowed to feed at the table after being trained to fly in through the window in the usual way. One group of three animals was then trained with the blue card rewarded and the other group with the yellow rewarded. The position of the cards were frequently interchanged / .....

FIGURE TWENTY-FIVE.
Learning curve for bees learning a visual discrimination.



/ interchanged during each training session.

The initial approach and landing of each bee was recorded. When a bee came in through the window it normally flew directly to one of the coloured cards and landed. If it had chosen the incorrect stimulus it found only water in the dish and flew off again. It then landed again on the same card or flew to the other one, or perhaps flew back out of the window. Bees landing on the correct card occasionally flew away again without feeding. Only the first inflight and landing of each bee was scored; the confusion of bees taking off and re-landing was ignored.

It took little time for the bee to return to the hive and unload its sugar supply. Generally an individual was back in the room again four to eight minutes after leaving. Thus it was possible to give every animal about ten trials an hour.

Results

The averaged results from both groups of bees are plotted opposite. The percentage of errors is drawn against trials. It can be seen that the bees very quickly come to visit the correct card exclusively. This is true whether the blue or the yellow stimulus is rewarded.

Experiment two

This second experiment tried out a method of training and / .....

/ and scoring which is claimed to give a very sensitive measure of the bees choice (Wehner 1968).

Materials and Methods

The same stimulus cards were used as in the previous experiment but this time they were presented in the vertical plane using the special training apparatus. Two groups of ten individually marked bees were used. One group was trained with blue positive and the other with yellow. In each case the training card was displayed in the top centre position of the apparatus and rewarded with two molar sucrose. A group of bees was allowed to visit the card for one hour. After this time the card was removed and the yellow and blue cards placed in positions equidistant from the central position previously occupied by the training card. Neither of these stimuli were rewarded. Bees now arrived, flew to one of the two cards and passed through the hole in the centre. They found only a vial of water and left again. They then re-entered or flew to the other card, or perhaps flew back out of the window. Occasionally, they approached one of the two cards but did not enter the chamber in the back. They sometimes just alighted on the face of the card or hovered in front of it. Coming up very close to a card (antennae within one millimetre), alighting, or alighting and entering were all scored as approaches. The total number of approaches to each card was measured over a five minute period.

Results / .....

/ Results

Bees consistently approached the card which had previously been rewarded in the central position of the apparatus. The results are tabulated below.

TABLE FOUR

Training figure yellow	Training figure blue
Total no. of approaches	Total no. of approaches
187	141
% approaches to yellow	% approaches to blue
91.4	91.1
% approaches to blue	% approaches to yellow
8.6	9.9

Conclusions

Two training and testing techniques were tried out. Both effectively demonstrated changes in choice behaviour and were used in later experiments. The second test is superior in that each bee makes a number of approaches on each flight. Large numbers of results can thus be accumulated quickly and small differences in preference may be detected. However, this technique can only be used when neither stimulus bears reward. In some experiments this may not be desirable.

14.

REVERSAL LEARNING AND CONDITIONAL REVERSAL LEARNING TASKS.

Introduction

In this section the behaviour of the bee on a reversal learning task and a conditional reversal learning task is described. These tasks are identical in form to the two problems on which the behaviour of the cockroach was investigated.

The significance of reversal learning has been discussed both in the general introduction and in the introduction to the equivalent experiments with cockroaches. Briefly, it has been shown that there is a systematic trend in the behaviour of animals on reversal learning problems. 'Higher' animals, e.g. primates, rats, birds, show a progressive increase in efficiency at learning successive reversals of a discrimination problem while 'lower' animals , e.g. fish, turtles, show no or very little improvement over a series of reversals. Among invertebrates tested, Octopus alone has been definitely shown to improve in discrimination learning as a function of reversals. Experiments carried out with the cockroach showed that it did not improve in its rate of learning over a series of reversals, except as a function of general experimental improvement.

The reversal tasks studied in this section are again visual ones, the animal learning to discriminate between a blue and a yellow card laid out on a table. In experiments on reversal learning, as in most discrimination problems, discrete / .....

/ discrete trials are given. In the experiments with the cockroach a T-maze was used and if the animal made an error it was removed from the apparatus and given another trial after a fixed time interval. In many experiments on reversal learning the animal has a choice of pressing one of two buttons. The fish will push against one of these buttons, the pigeon peck and the rat press with its feet or head (Bitterman 1965). In a situation like this, discrete trials are arranged by following an error or a reward with a period of time during which the apparatus is blacked out. The length of this 'time-out' period determines the length of the inter-trial interval. Without this period it would not matter much to the animal whether its choices were correct or not as it could immediately correct an error at the expense of little effort. The time out period after error delays a chance to have access to the reward again and prevents the animal from responding randomly.

A simple way of giving the bees discrete trials was devised so that the method was strictly comparable to that used in all other reversal learning experiments. The bees had to discriminate between two differently coloured cards, one bearing sucrose reward and the other not. If a bee makes an incorrect choice it finds no reward and takes off again. At this point a large black card is placed over both training cards so that they cannot be seen by the animal. After a time interval of three minutes the stimuli are uncovered again. If the bee makes a correct choice, the apparatus is covered for three minutes after the animal has finished drinking and flown away.

Apparatus / .....

/ Apparatus

The bees had to discriminate a blue from a yellow card. These cards were the same as used in the previous experiment and are known to be easily discriminable and approximately equally attractive to the bees. Both cards were covered by a sheet of glass. One card carried reward in the form of a clear plastic dish containing two molar sucrose, the other card had an identical dish containing water placed above it. A large piece of black card, 70 cms. x 70 cms., could be placed over the stimulus cards and dishes to hide them from view.

Methods

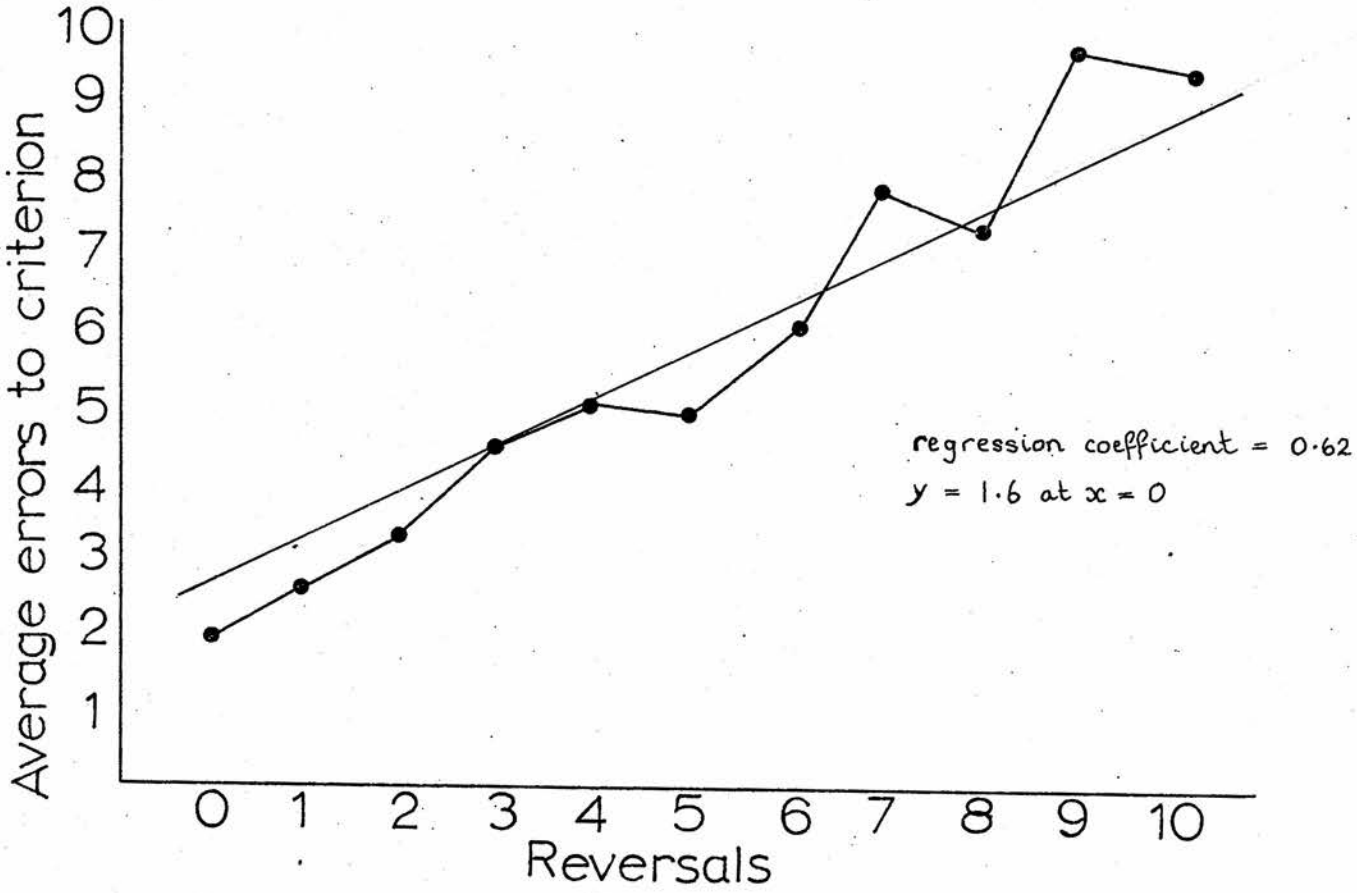
The two cards were laid out on a black table fifteen cms. apart and at right angles to the line taken by the bees entering through the window. Eight bees were individually trained on a series of discrimination reversals. One card bore the reward until the animal showed nine out of ten initial approaches to this stimulus, i.e. until on nine out of ten occasions the bee flew in through the window and first approached this card. When this criterion was reached the reward was switched to the other card and so on. Training began early in the day and continued until nightfall, further training then began again the next morning.

The positions of the cards were interchanged every twenty minutes to prevent positional information influencing the bees choice. Whenever the positions of the cards were changed the glass plate covering them was wiped with alcohol and clean dishes of sugar solution and water laid out to replace those already in use.

Results / .....

FIGURE TWENTY-SIX.

Graph showing errors to criterion over a series of reversals of a visual discrimination.



/ Results

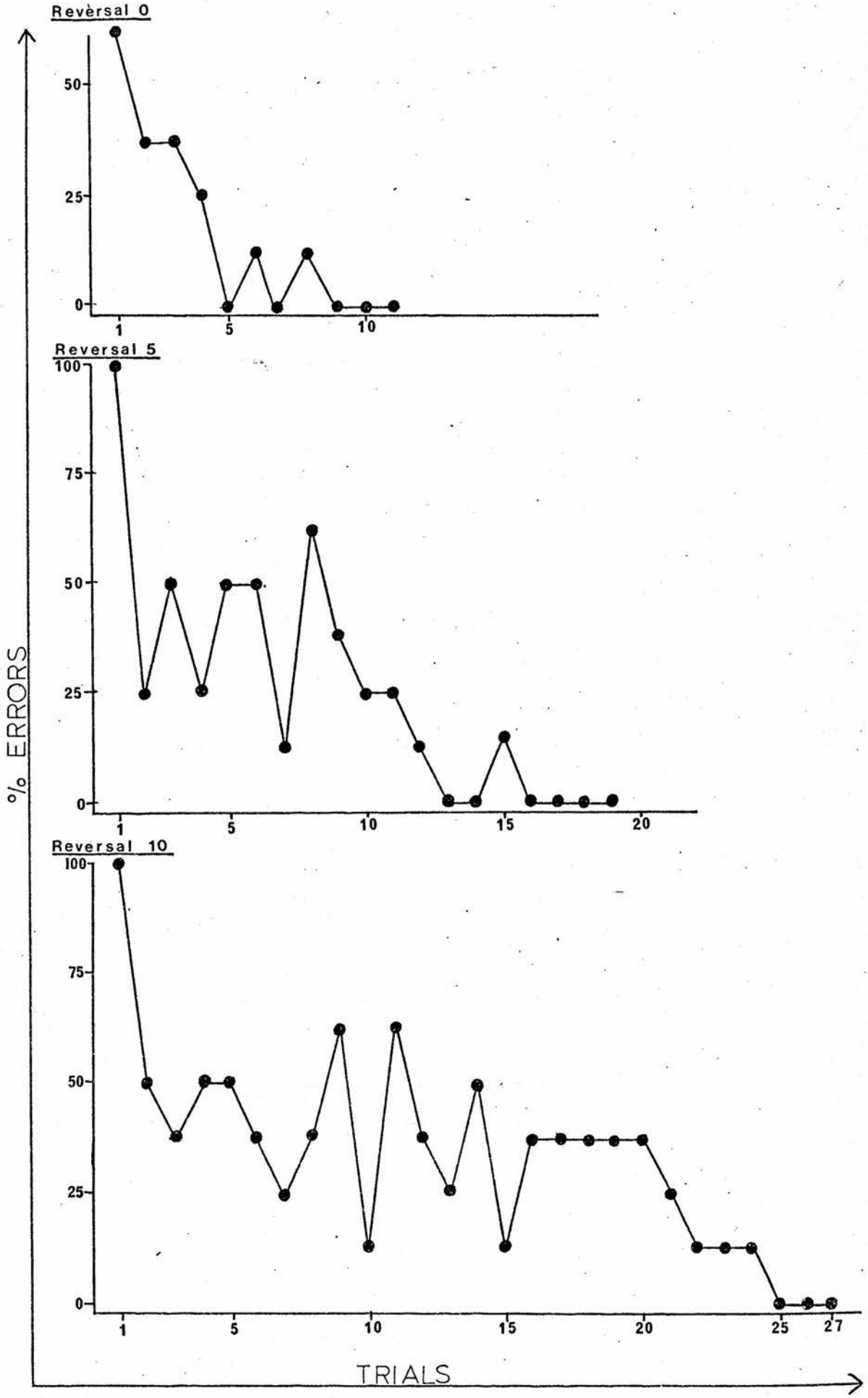
The results were rather surprising. All eight bees showed a steady increase in the number of errors taken to reach criterion with successive reversals. The average number of errors to criterion plotted against reversals is shown in figure twenty-six. Each point on this graph represents the average number of errors taken to reach criterion for the entire group of eight bees for a particular reversal. Initially, bees took only a mean value of 1.9 errors to reach criterion but the tenth reversal they were making a mean of 9.5 errors to reach the same criterion. Bees thus behaved in quite the opposite way from cockroaches. Bees began at a level of performance better than ever reached by the cockroach and after a series of reversals performed nearly as badly as the cockroaches did initially. The changes taking place in the bees behaviour can be seen in more detail by comparing the initial learning curve with those of later reversal 0, 5 and 10. In each the average percentage errors for the group of eight bees is plotted against trials. Each point thus represents an average of eight results.

It can be seen from the initial learning curve, reversal 0, that bees very quickly learnt to approach the rewarded stimulus. By the fifth reversal a great change has taken place in the form of this learning curve. On the first trial, all the bees made errors as they all approached the previously rewarded stimulus. However, on the second trial a dramatic reduction in errors was seen and for the next seven trials the percentage errors remained around the fifty

per cent / .....

FIGURE TWENTY-SEVEN.

Reversal learning: learning curves for reversals 0, 5, and 10.



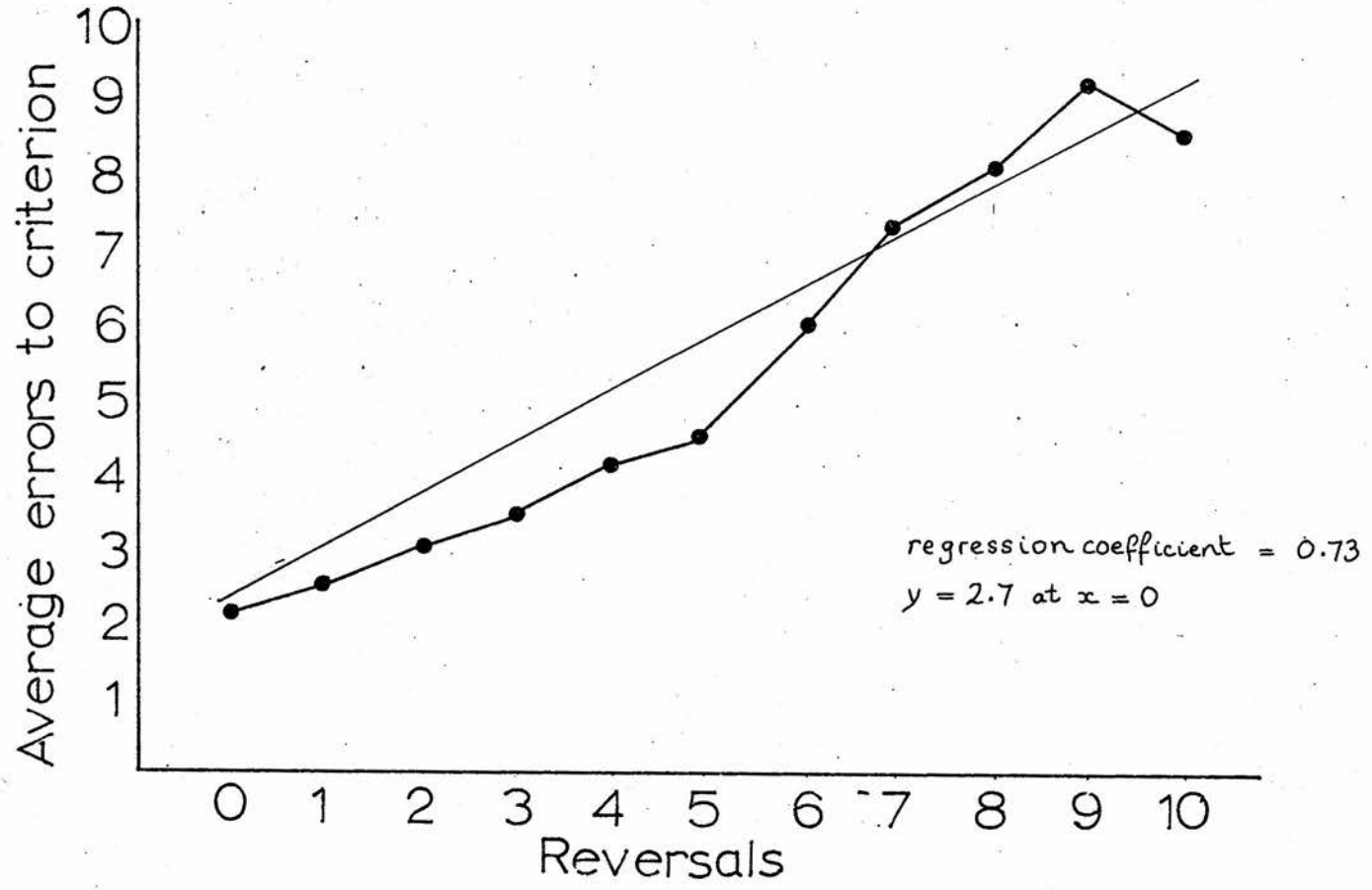
per cent level. Finally, a gradual reduction of errors occurred and the bees reached criterion. What is remarkable about this behaviour is the rapid drop in errors to the chance level followed by the gradual elimination of errors to the zero level. These two phases are even more pronounced by the tenth reversal. On the first trial 100 per cent errors were made, and on the second 50 per cent, followed by a long phase in which bees visited the two cards equally often and then gradually eliminated errors. The long phase of 50 per cent errors was not due to some bees visiting one card exclusively and some the alternative so that on average both cards were visited equally often. Each bee, as shown for a representative individual in Appendix 8, passed through a phase of visiting the two stimuli equally often. It appears that with increasing number of reversals bees find it progressively more difficult to visit one card exclusively. Further discussion of these results is delayed until after the conditional reversal discrimination has been considered.

A Conditional Reversal Task

The materials and methods of this experiment were identical to the previous one except for the provision of an additional cue. The background area around the two stimulus cards could be either black or white. Two sheets of cardboard were used, each 50 cms. x 30 cms., so that a large area surrounding the two stimulus cards could be varied. Whenever the background was white the blue card carried reward, when it was black the yellow card carried reward. / .....

FIGURE TWENTY-EIGHT.

Graph showing errors to criterion over a series of reversals of a conditional visual discrimination.



/reward. Bees were trained to a criterion of nine correct approaches out of ten on one card, then the background was changed and the reward switched to the other card until criterion was again reached and so on. Eight bees were individually trained as in the previous experiment. Once again, discrete trials were arranged by covering the stimulus cards with a sheet of black cardboard for three minutes after error or reward.

Results.

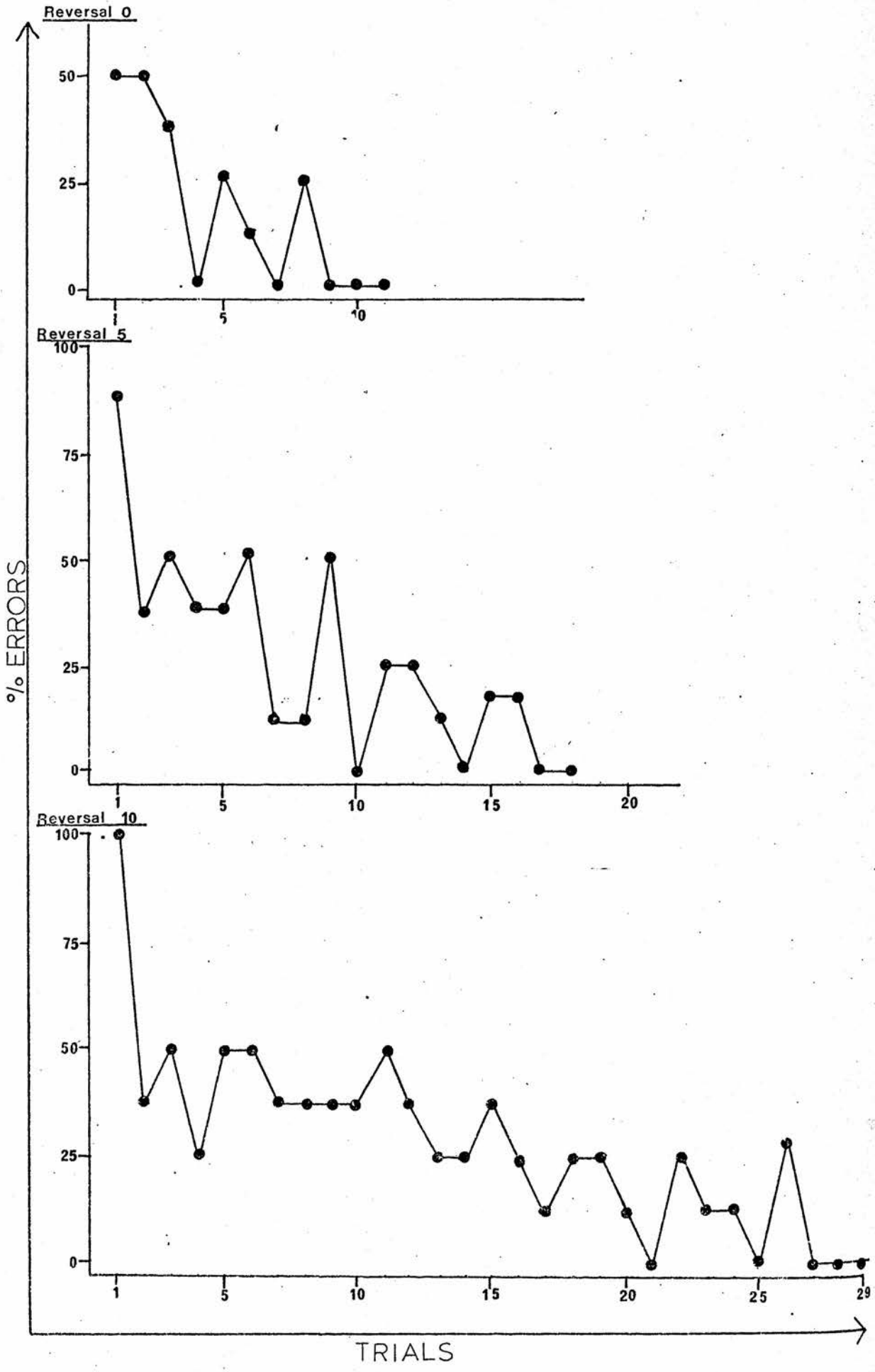
On this discrimination also the bees took progressively longer to reach criterion with successive reversals. The provision of the extra cue had no effect upon the bees behaviour in this respect. The average number of errors to criterion is plotted against reversals in figure twenty-eight. It can be seen that the results are very similar to those derived from the first reversal learning experiment. To check for any differences between these two sets of results the coefficient of linear regression was calculated for each set of data. The regression lines are represented on each graph by a dotted line and the coefficients of linear regression and associated constants shown alongside. The variance of each of the two regression coefficients was then calculated and the two distributions compared (Bailey 1959). No significant difference existed between them at the ten percent level of significance (experimental d=1.26, d=1.64 at ten percent level) and thus the rate of change of errors to criterion with reversals may be assumed to be unaffected by the addition of a second cue. (See Statistical Appendix II).

A similar pattern of changes was also found in the learning curves for particular reversals. Learning curves averaged for the group of animals are plotted in figure twenty-nine for reversals 0, 5 and ten. As in the previous experiment, late reversals showed a rapid initial fall in errors, a long phase during which the bees vi ited both cards equally often and finally a gradual elimination of errors. The results of this experiment are thus identical to the previous one;

the/

FIGURE TWENTY-NINE.

Conditional reversal learning: learning curves for reversals 0, 5 and 10.



/ the previous one; the provision of an additional cue appears to have no effect upon the bees behaviour.

Discussion

An experiment on reversal learning in bees was published shortly after the experiments described here were carried out. Menzel (1969) trained bees on a similar visual reversal problem but instead of training individuals to criterion he trained groups of bees for fixed times on each option. He found that after four or five reversals the bees began to choose both colours equally often. Similarly, in a reversal problem in which two odour cues were used (Koltermann 1969) bees quickly came to visit both odours equally often.

The pattern of behaviour seen in these experiments, a rapid reduction in initial errors followed by a long phase of random responding, has not been observed in any animal other than the bee. How does it fit in to theories attempting to explain reversal learning ?

Proactive inhibition theories suggestthat with reversals it becomes increasingly difficult for the animal to remember which cue was last rewarded. After a number of reversals bees show phases during which they approach both cues equally often. However, this effect cannot be due to pro-active inhibition because on the first trial of a reversal, no matter how late in the series, the bees respond exclusively to the previously rewarded cue. There is thus no defect in their retention as they clearly remember which cue was last correct at the beginning of the reversal session. Had they also / .....

/ also shown a random choice at the beginning of the session then proactive inhibition would have been a viable explanation.

Attentional theories predict two possible reasons for a failure to improve over a series of reversals. Animals may not maintain attention to the correct stimulus dimension after reversal and may instead attend to irrelevant cues such as position. In the experiments with bees, only by attending to colour cues could the animal consistently obtain reward. However, although no improvement may be seen as a result of this failure to consistently attend to the correct dimension, there is no reason to suppose that animals should actually deteriorate over a series of reversals, as a result of failure to maintain attention to the correct stimulus dimension. The theory would simply predict that the animal would have to once more re-learn the correct dimension as it did when initially presented with the problem. A progressive increase in the number of errors to criterion with reversals would not be predicted.

Attentional theory would predict a progressive deterioration in performance if the animal maintained attention to the correct stimulus dimension but strongly attached responses to one value of the dimension. The animals would then begin a reversal with preference to go on responding to the previously rewarded colour. It was shown in the experiments on reversal learning in the cockroach that the animal had difficulty in switching responses from one stimulus value to another on reversal and thus scored a high number of initial errors. However, in experiments with the bee it was seen that after only one trial the preference for the last reward / .....

/ rewarded cue vanished entirely. In conclusion, neither proactive inhibition nor attentional effects as presently understood can explain the form of the changes seen in the bee's behaviour on a reversal task.

The behaviour of the bee on these problems is perhaps not surprising when we consider its natural life. Bees learn to visit flowers which are producing nectar or pollen and, as shown by the initial learning of the colour discrimination, can very quickly learn to associate a particular colour with reward. In the reversal experiments two different 'flowers' alternately bear reward. Real flowers also bear reward at some time but not at others. Many flowers show a pronounced diurnal rhythm of pollen and nectar production. In the reversal experiments, whether a 'flower' was producing reward or not did not depend upon time but upon the performance of the bee on the learning task. A switch of reward from one stimulus to another was not signalled by a time of day or sun position cue but by either non-reward or a change in the background colour of the stimuli. When a time-of-day cue does determine which of two stimuli is rewarded, bees learn to switch from stimulus to stimulus without difficulty. A recent experiment demonstrates this clearly. Bees were trained to discriminate a pair of food dishes marked by different odours. This training was carried out at a particular time of day. When bees were tested at an earlier time the following day they appeared to remember nothing of this training. However, as the training time approached, bees more and more preferred this odour until at the training time / .....

/ time they visited it exclusively. Once the training time had passed the preference for the odour waned once more (Koltermann 1969, 1970). Bees have been trained to visit each one of a set of six odours at different times of day in this way. Similarly, Finke (1958) was able to train bees to visit four different feeding places at different times of day.

In a natural situation where the foraging of bees on two adjacent crops has been studied, bees were found to display wide and consistent variations in the proportions of the flowers of each species which were visited at different times of day. These variations could be ascribed to the choices of the bee following changes in the relative attractiveness of the flowers (Ribbands 1949). Some bees even worked both nectar and pollen producing crops and switched from collecting nectar to pollen at a particular time of day. Thus a problem of the same logical structure as the conditional reversal problem, a problem in which reward alternates between two stimuli and this is signalled by another cue can be easily solved by the bee when the cue is time of day (or sun position).

It seems probable that the bee has evolved specific learning capabilities to enable it to follow the temporal rhythms of nectar and pollen production in different species. These abilities are not well adapted to the 'general intelligence' type reversal learning problems. In these problems the bee finds changes in reward uncorrelated with time, / .....

time, a situation it does not meet in its natural life. Clearly, very little can be understood about the learning ability of the bee if its behaviour on a reversal learning task is considered in isolation from the conditions of its natural life. Although the bee is the only animal known to show a consistent, large deterioration in performance over a series of reversals of a discrimination its learning ability is beautifully adapted to the conditions it meets in its natural life. Such considerations must show that it is not useful to attempt to apply concepts of 'intelligence' or to attempt to measure a general 'learning ability' by standard tests in the bee.

15.

VISUAL DISCRIMINATION AND CONCEPT FORMATION.

FIGURE THIRTY.

Honeybees could distinguish the figures in the top row from those in the bottom row with ease. They could not tell apart the figures in either the top row or the bottom row (Hertz 1929).

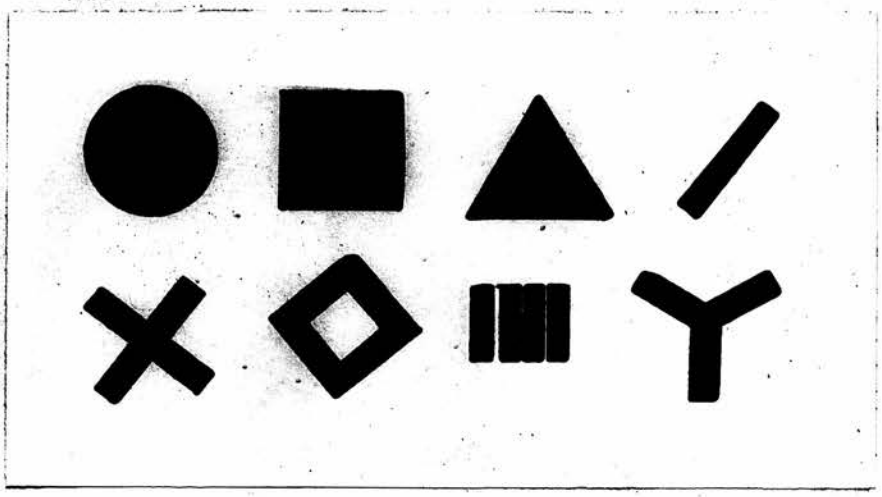
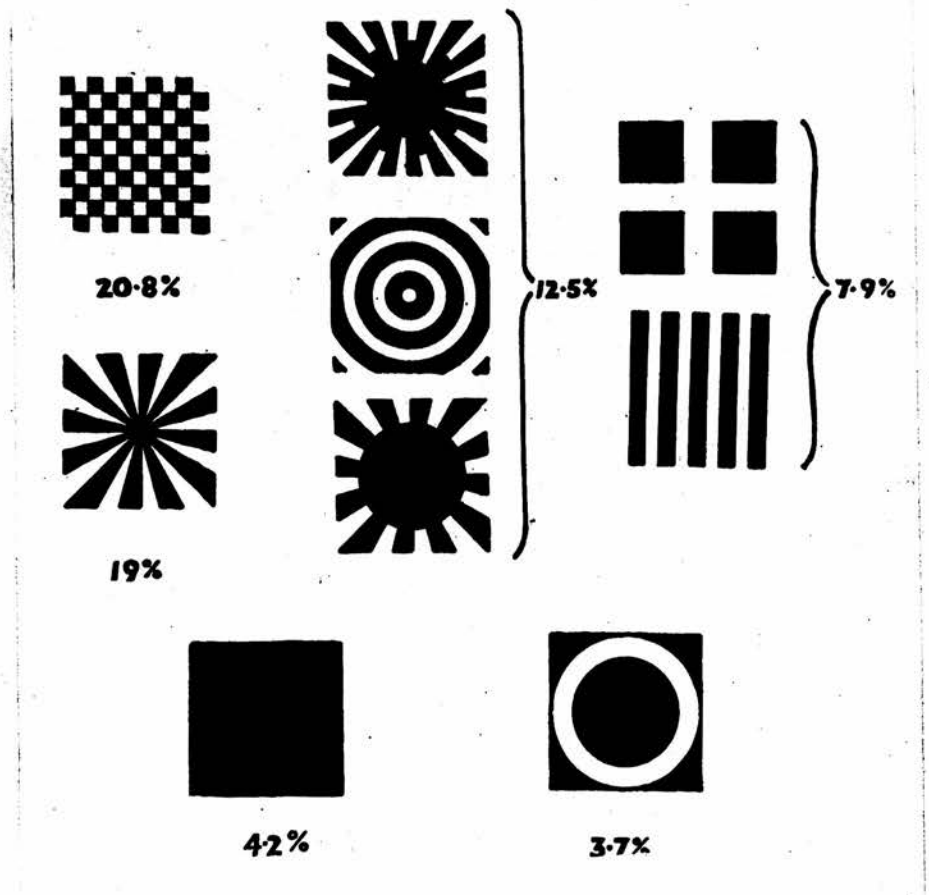


FIGURE THIRTY-ONE.

Honeybees were presented with these patterns without previous training. Their spontaneous preference is shown by the percentage of choices they made to each figure in 226 tests. (Zerrahn 1933).



This final set of experiments was inspired by the work on concept formation in bees carried out by Mazochin-Porshnyakov (1969 a,b,c). He claimed that bees have an ability to construct visual concepts equal to that found in higher mammals. Possibly this capability is a specialised adaptation pre-requisite for the remarkable orientation performance of bees and for their visits to flowers. However, previous research on visual discrimination in bees had suggested rather a different story.

A large body of work on the capacity of the bee to learn to discriminate different shapes was carried out around the 1930's. Hertz (1929) suggested that in discriminating shapes the bee relied upon the parameter of 'figural intensity'. This is a measure of the amount of contour or outline per unit of area of the shape. A striped of divided figure will contain a large amount of dark/light contour per unit area and will thus have a high figural intensity as compared to a plain, simple figure which will have contour only at its edges. This one parameter appeared to be so important that bees were found unable to discriminate shapes which were of similar figural intensity. In the set of shapes shown in figure thirty, Hertz found that bees could not discriminate between any of the figures within the top or bottom rows but could easily be trained to discriminate any figure in the top row from any in the bottom. The figures in the top row are simple ones of similar low figural / .....

/ figural intensity and those in the bottom row are more divided figures of a higher figural intensity. Despite their dissimilarity to us, the bees could not be trained to discriminate between the triangle, square and circle shown.

In choice situations bees were found to have a spontaneous preference for the shape of highest figural intensity (Zerrahn 1933), although this could be reversed by training (Hertz 1933). If given an array of chequer-board patterns to choose from they were found to visit most frequently the one containing the highest number of sub-divisions in a unit area (figure thirty-one), provided the small squares were not so small as to be indistinguishable to the bees eyes (Zerrahn 1933). Similarly, if a bee had been trained to a cog-wheel pattern as opposed to a disc, it was found that it would transfer its attention from the cog-wheel if the disc was replaced by another cog-wheel with more teeth and thus more contour per unit area than the first (Hertz 1929).

The structure of the compound eye of the bee seems well suited to abstract this dimension of figural intensity. As a bee flies over one of these patterns each ommatidium will be stimulated as it passes over a light/dark boundary. Clearly, the more boundaries a figure contains the more on/off 'flicker' stimulation will the bees eyes receive. It has been shown that if bees are permitted to choose between two patches of flickering light both of the same intensity but of / .....

FIGURE THIRTY-TWO.

Bees trained to A1 went equally to c1, to A2 equally to B1 and C2. But bees trained to C1 or 2 would not visit A1 and one trained to D2 ignored A2. Thus in some cases bees will visit figures of shorter outline. The numbers give an index of the length of outline of the figure (Hertz 1933).

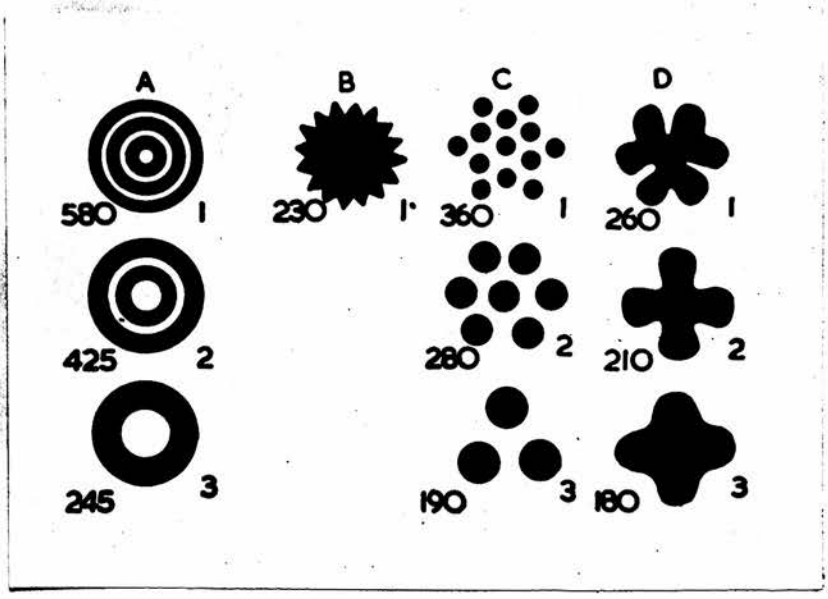
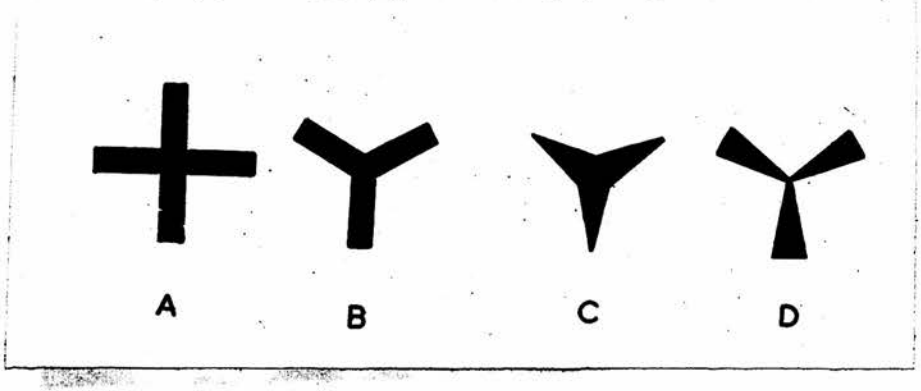


FIGURE THIRTY-THREE

A was found to be interchangeable with B without confusing the honeybee. Replacing either one by C caused confusion, however, though the same triangular pieces in a different arrangement, D, did not cause confusion.



of different frequencies they visit each light in proportion to its flicker frequency (Wolf 1934). The faster the light flickered the more approaches are recorded up to the flicker fusion frequency for the bee's eye.

Obviously, moving figures will generate more 'flicker' than stationary ones of the same figural intensity. Bees have been shown to find moving figures more attractive. When one half of a bed of artificial flowers was waved back and forth while the other half was stationary, the moving half was found to attract to twice as many bees (Wolf 1937).

So strongly do bees prefer a more highly divided figure that it is difficult to train them to visit the less highly divided figure of a pair. Indeed, at one time it was claimed to be impossible (Zerrahn 1934) but in figure thirty-two are shown a couple of examples in which this was achieved. Bees trained to the set of small discs would not visit the three concentric circles, nor would ones trained to the two concentric circles visit this figure although in both cases they are choosing figures of lower outline/unit area.

Responding to the parameter of figural intensity is adaptive in terms of the bees life history. Beds of flowers present highly divided forms and their attractiveness is increased by patterns on the petals. Different species of flowers will have different characteristic figural intensities.

Figural / .....

/ Figural intensity was postulated as the parameter used by the bee because it explained why the bee could not discriminate certain shapes and why some shapes appeared more similar to it than others. This way of generating models of the mechanism of form perception has been used systematically in a series of experiments on Octopus, (Sutherland 1960). Sutherland points out that shapes differ from one another along a number of different dimensions. Examples of dimensions or parameters of shape are area, length of outline, vertical extent of shape, vertical extent relative to area, horizontal extent, ratio of vertical to horizontal extent, number of re-entrants, number of corners, figural intensity and so on. Different species might be expected to abstract different parameters and use them in classifying and judging the similarities of shapes. Bee appears to use figural intensity while for Octopus the ratio of horizontal and vertical extents appears to be the most important characteristic of shape. We can suggest theories about the parameters an animal is using by investigating the degree of similarity it sees between various shapes. It is possible to assess degree of similarity of different shapes for a particular species by the following methods.

(a) What shapes can the animal tell apart and how easily can it learn to tell apart different shapes ?

(b) What shapes is it impossible for the animal to discriminate between i.e. what shapes does it see as identical.

(c) / .....

/ (c) When the animal has learnt to discriminate particular shapes, what shapes will it generalise to, i.e. see as having some degree of similarity ?

The method is essentially one of trying out discriminations, erecting a hypothesis about the nature of the parameters used by the animals, making predictions about how the animal should perform on other discriminations, testing these, modifying the theory etc. Three complications must be mentioned in this approach.

(a) It is not possible to change shapes in only one parameter at a time or to have two shapes which differ from one another with respect to only one parameter. Changing a shape always results in changes in several different parameters.

(b) Animals might be expected to use more than one parameter at a time, or to switch from one parameter to another in different discriminations.

(c) Different species have preferences for particular shapes. It has already been mentioned that bees have a preference for shapes of high figural intensity; Octopus has a preference for shapes moving along their long axes (Sutherland 1960). When discrimination and generalisation tests are performed it is necessary to take into account the spontaneous preferences of the animal.

Although / .....

Although, as discussed earlier, experiments along these lines have postulated that the parameter of figural intensity is used by the bee to discriminate shapes, some discriminations performed by the bee are quite inexplicable on the basis of this parameter alone. For example, in figure thirty-three, bees were trained to discriminate shape A from a disc. When shape A was replaced by B or D bees accepted these shapes in preference to the disc. However, when the same units of D were re-arranged in combination C the bees refused to visit this shape (Hertz 1929).

Recent research has clearly shown that the parameter of figural intensity does not always govern the bees choice. Wehner (1966; 1967a,b; 1968) has been able to show that bees can be trained to discriminate between different inclinations of black stripes offered on a white screen. The model he proposes for this discrimination and for that of simple geometrical figures is that the bee's visual system detects the spatial distribution of black and white areas within the visual field as it approaches the test shapes. During training it is postulated the bee learns which regions of its visual field are respectively black and white and compares this with other distributions of black and white areas presented in tests after training; the less the positions of the black and white areas in a particular test pattern coincide with their positions during training, the better the discrimination between the two situations.

Later experiments (Wehner 1971) showed that the information abstracted by the bee is in a more general form / .....

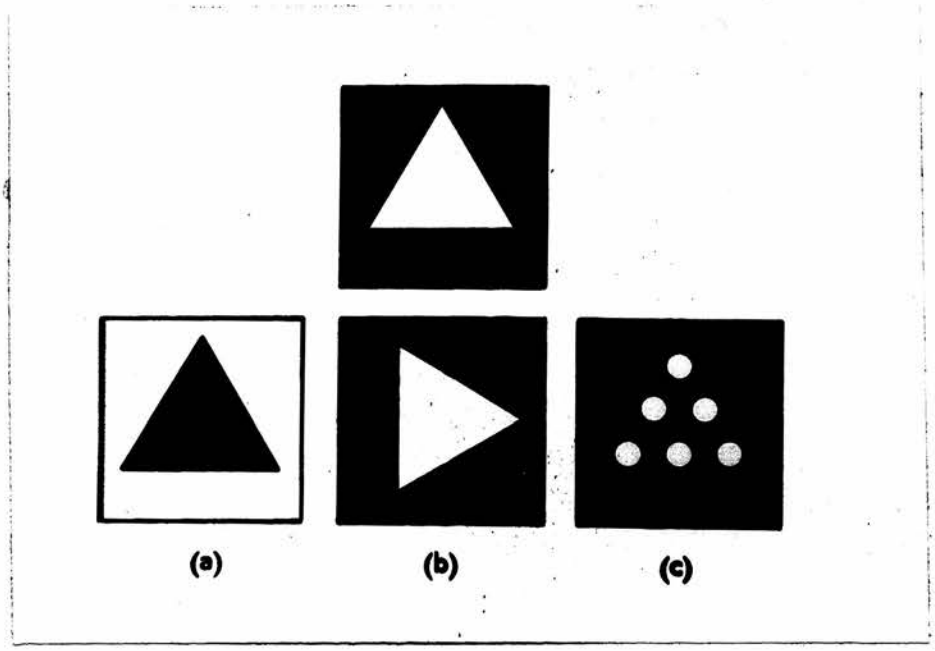
/ form than simply the distribution of black and white areas because the discrimination persists even if the contrast of the stripes is totally reversed. Wehner also demonstrated that bees could be 'trained along a contimuum'. He showed first that bees did not easily discriminate short stripes of differing orientation. However, if they were initially trained on a long stripe of the same orientation they became much better at discriminating the short stripes, the 'attention' of the nervous system had apparently been shifted towards that parameter. This effect of improved discrimination after training on other stimuli that have a larger difference along the same dimension had previously been demonstrated only in mammals and the Octopus. These experiments led Wehner (1971) to speculate that 'there may not be as large a gap as so far assumed between the higher recognition and learning performances in vertebrates and invertebrates'.

Research carried out in Russia by Mazochin-Porshnyakov (1969 a,b,c) led to a much more remarkable estimate of the bees learning capability. He suggested his investigations 'lead us to the conclusion that it is permissable to speak of intelligent behaviour in bees'. His investigations are claimed to show that bees were able "to process in the CNS not only according to shape but according to more difficult viewpoints such as'multi-coloured and chequered' or 'position of test objects relative to other objects.' " His main experiments showed the following points:

1) / .....

FIGURE THIRTY-FOUR.

The concept of 'triangularity' in some different animals. Trained to respond to the top figure, a rat makes random responses to any of the lower figures. A chimpanzee responds to a) and b) but makes random responses to c). A 2-year old human child recognizes a triangle in a), b) and c) (Hebb 1958). According to Mazochin-Porshnyakov the bee would also recognise all these figures as 'triangles'.



1) Bees could be trained to discriminate a triangle from a square and this discrimination was maintained when the shapes were altered in size, orientation, colour, background colour and form of outline. This level of performance is not reached by many mammals. In figures thirty-four is shown the concept of 'triangularity' for several other animals. It can be seen that even rats have difficulty in generalising from an upright triangle to one rotated through ninety degrees. According to Mazochin-Porshnyakov (1969a), all the shapes in figure thirty-four would be recognised as triangles by the bee. He also showed that the discrimination between a triangle and a square will persist even when one adds 'visual noise' by scribbling over them and adding ink blots (mazochin-Porshnyakov 1969b).

2) Bees could be trained to pick out the 'chequered' shape from a set of shapes. This discrimination persisted when the colour of the objects was changed.

3) Given a set of hollow shapes each with a little square either inside or outside them, bees could be trained to visit the 'square-outside' one irrespective of the actual form of the shape.

The experiments described in this thesis concern the first and third of these situations. Attempts to replicate and extend them were made firstly because Mazochin-Porshnyakov generally ascribed his results to 'intelligence' and did not attempt to find out on what basis the bee performed these discriminations and secondly because some important / .....

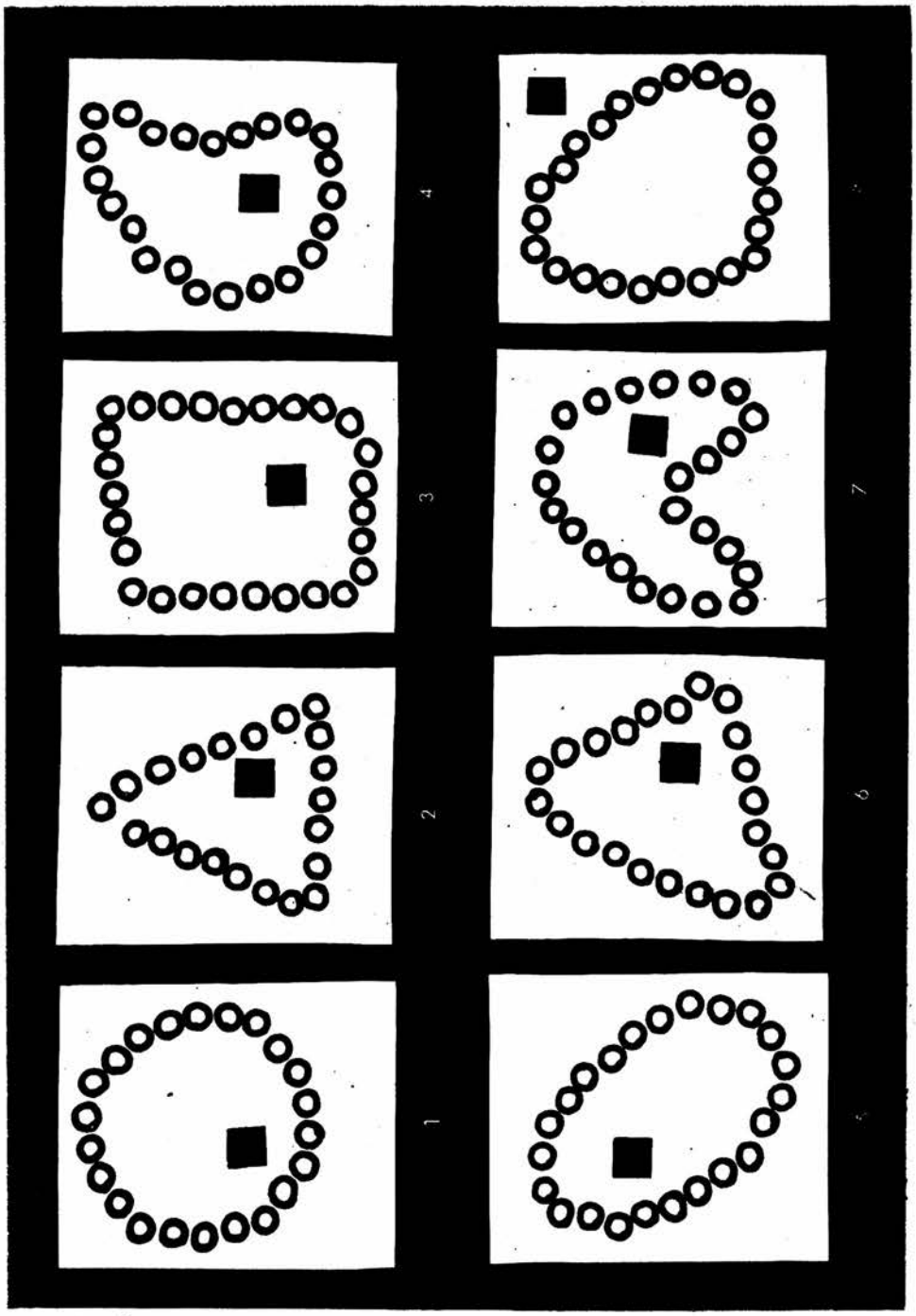
important controls were missing from his experiments. A more detailed analysis of each of his experiments is given in the following pages.

16.

THE CONCEPT OF 'OUTSIDENESS'.

FIGURE THIRTY-FIVE.

Training figures for experiments on the concept of 'outsideness'.



Introduction

In figure 35 are shown a set of training figures very similar in design to those used by Mazochin-Porshnyakov (1969a,b). In his experiment he displayed this array to a group of bees and rewarded the shape with the little square outside it; in the unrewarded figures the square is always inside the shape. After training, bees were tested on the same array but with the little square outside a different shape. None of the figures were rewarded in this test and the number of approaches to each figure was measured. At first bees showed no preference in this test but after a series of training sessions in which several of the shapes had had the square outside and had been rewarded bees began to show a strong preference for the 'square-outside' shape in the tests. He showed that this preference emerged after as few as three of the shapes had had the square outside and had been rewarded. He thus claims that bees are easily able to form a concept of 'square-outside-shape' and that once this concept is acquired bee can respond to this parameter in a variety of shapes. Mazochin-Porshnyakov cites this experiment as evidence of 'intelligence' in bees. He does not attempt to analyse how the bee performs this subtle discrimination.

In the experiments described below an attempt was made to replicate the work of Mazochin-Porshnyakov so that an attempt / .....

/ attempt could be made to analyse the parameters used by the bee in making this discrimination. It may well be that the honey-bee uses some parameter other than 'outsideness' to solve this problem, e.g. whether the black square is near or far from the centre of the card. The bee does not necessarily acquire a concept of outsideness in our own sense.

Apparatus

The array of stimulus cards is shown in figure thirty-four. They are drawn upon the usual standard sized test cards. The small black square was attached by a pin so that it could be moved inside or outside its accompanying figure. The experiment was performed with the cards displayed both horizontally and vertically.

Methods

Forty bees were individually marked and allowed to take part in the experiment. A fresh set of forty bees was used for each repeat of the experiment.

The method used replicates that of Mazochin-Porshnyakov as closely as possible. An initial training array was set up as shown in figure thirty-four and the figure with square outside rewarded with two molar sucrose. Every fifteen minutes the positions of the cards were changed in a random fashion. After one hour's training the bees were given a test. The training array was replaced with a test array in which a different figure hadthe square-outside. None of the shapes were rewarded. The initial approach of each of the forty bees as they fly in through the window was recorded. A new training array was then arranged and the whole procedure was repeated / .....

TABLE FIVE.

THE CONCEPT OF OUTSIDE/INSIDE.

Total number of approaches to each of the eight test figures over a series of sixteen tests.

Horizontal plane.

Stimulus no.	No. of approaches.
Correct stimulus - 1	70
2	84
3	81
4	77
5	67
6	62
7	74
8	71

Vertical plane.

Stimulus no.	No. of approaches.
Correct stimulus - 1	57
2	61
3	65
4	66
5	67
6	61
7	65
8	51

Total number of approaches to each of the eight test figures over a series of eight tests in which the test figure was always the same as the training figure

Stimulus no.	No. of approaches.
Correct stimulus.—1	29
2	28
3	34
4	31
5	26
6	31
7	25
8	33

/ repeated, in each set of training figures a new shape had the square outside. In the test arrays the same figure always had the square outside.

This procedure was repeated for sixteen training periods and as there are eight stimulus cards, every shape had had its square outside and been rewarded twice. This sequence was carried out once with the figures in the horizontal plane and once with the figures in the vertical plane.

Results

The results are shown in table five. During the tests the shape number one always had its square outside. The total number of approaches to each of the eight shapes over a series of sixteen tests is tabulated. These results are for the whole group of forty bees. It can be seen that, contrary to the results found by Mazochin-Porshnyakov, the square outside figure is not significantly preferred even though there have been some sixteen training periods, far more than used by him. This is true both of the experiment conducted in the horizontal plane and that carried out in the vertical plane.

After this failure to replicate Mazochin-Porshnyakov's results, a simpler experiment was tried to see if the bee could pick out the correct figure when a long period of training was given on just one of the shapes.

Methods

This experiment was basically the same as the previous one but the same shape always had its square outside and was rewarded during the training sessions. This shape also was the square-outside shape in the test periods. All that was changed / .....

/ changed between sessions was the position of the training/ test figures. Thus bees could have picked out the square-outside figure on the basis of its shape or its 'square-outsidedness'. A group of forty bees was trained for eight training and test sessions according to the method above.

Results

The results are shown at the bottom of table five. Once again the total number of approaches to each of the eight test figures is tabulated for the entire group of forty bees. Once again the bees did not significantly pick out the square-outside figure even though it was identical to the one they had received eight hours training on. Thus it appears the bees cannot even tell the set of shapes apart, let along form a concept of 'square-outside' which is independent of the actual shapes involved.

It was observed that on tests the bees appeared to visit the previously rewarded position rather than taking any notice of the significance of the shapes. When the results were analysed in these terms it was found that 63% of all approaches in the test situations were directed towards the place where reward had last been found. Over the sixteen training and test periods the positions of the training and test figures had been varied so that on average all the positions and all the shapes received an equal number of visits as shown in table five. Thus, although positions of the training cards were varied every fifteen minutes during training, the bees succeeded in acquiring only positional information about the whereabouts of reward.

Conclusions / .....

/ Conclusions

A repetition of Mazochin-Porshnyakov's experiment failed to find any evidence that bees could acquire a concept of inside/outside. Far more intensive training was given than in the original experiments. In the experiments reported here positional information primarily controlled the bees choices in the test situation. These experiments were conducted indoors in a laboratory and there were thus numerous objects close to the test apparatus which could have been used by the bees for orientation purposes. The experiments of Mazochin-Porshnyakov were conducted out of doors where there were quite possibly few near-distance landmarks. Possibly the bees did not form concepts in my experiments because there were too many positional cues which prevented them from attending to the visual cues. Different strains of bees have been shown to have pronounced differences in the extent to which they rely upon near-distance landmarks (Lauer and Lindauer 1971). It is thus possible that my bees were very 'positional' ones and did not attend to the shape cues, this accounting for the difference between these results and those of Mazochin-Porshnyakov. Unfortunately, he does not describe his methods or results in sufficient detail for an exact replication of his experiments to be made. Under the conditions possible at Edinburgh no evidence could be found that honey bees Apis mellifica mellifica could form a shape concept of outside/inside.

17.

THE CONCEPT OF 'TRIANGULARITY'.

Introduction

Mazochin-Porshnyakov claims to have shown that bees can be trained to discriminate a triangle from a square and that this discrimination persists when the shapes are changed in size, orientation, colour, background colour and form of outline, i.e. solid or broken. He claims that these results demonstrate 'concept formation' in the bee. No attempt was made to analyse the parameters used by the bee in recognising 'triangles' and 'squares'. His research was conducted in Russia and stems from a school of thought different from that of Western behavioural science; he seems more concerned with demonstrating 'intelligence' than with finding out how the bee performs these discriminations For example, in one experiment he shows that the bee can discriminate a triangle from a square even when he has covered them with scribbles and ink blots, this - he claims - demonstrates that the bee must be very intelligent. In the series of experiments reported here* an attempt was made to replicate some of the findings of Mazochin-Porshnyakov and to try to discover the parameters used by the bee in carrying out these discriminations and generalisations.

The / .....

* These results are also reported in "The ability of the honey-bee to generalise visual stimuli" by A.M. Anderson in "Information processing in the visual system of Arthropods", published by Springer-Verlag, Heidelberg 1972 (in press).

/ The simplest explanation of his results would be that only one parameter of shape is detected in the whole series of discriminations; a parameter on which all the triangles consistently had a different value from all the squares. This explanation would seem unlikely because so many transformations of the figures were made that no one parameter, other than 'shape', is likely to have remained unchanged throughout the experiment. However, this explanation cannot be entirely ruled out. In Mazochin-Porshnyakov's experiments he trained a group of bees to visit the triangle of a triangle and square pair. He then replaced the figures with a transfer pair of shapes and always found that the bees significantly preferred the new triangle to the new square. From this he claimed that the bees 'generalised' from one triangle to another different one and thus had some concept of 'triangularity'. At no stage in his experiments did he show that the bees could discriminate a training triangle from any of the transfer triangles. This is a very important point. If he had shown that the bees could tell apart the members of a set of triangles but also responded to them as being similar, then his claim that the bees had a concept of 'triangularity' would be supported. As he did not, it remains possible that the bees could not discriminate any of the triangles from a square. Clearly, if an animal sees a set of shapes as being identical in all respects it cannot be claimed that the animal has a 'concept' of that particular shape. Rather, it may merely be responding to one feature, or one value of a particular parameter, that all these shapes have in common. This / .....

/ This control experiment, of checking to see that the bees could discriminate a training figure from a transfer figure, an experiment essential if the claim that animals 'generalise' between two figures is to be entertained, was never carried out by Mazochin-Porshnyakov.

In the first experiment to be described one of Mazochin-Porshnyakov experiments is repeated with additional controls to see if the bee is truly generalising to transfer figures or is merely seeing them as identical. Further experiments then attempted to analyse the parameters used by the bee in making these discriminations.

Experiment one: Generalisation between triangles differing in size, orientation and sub-unit size.

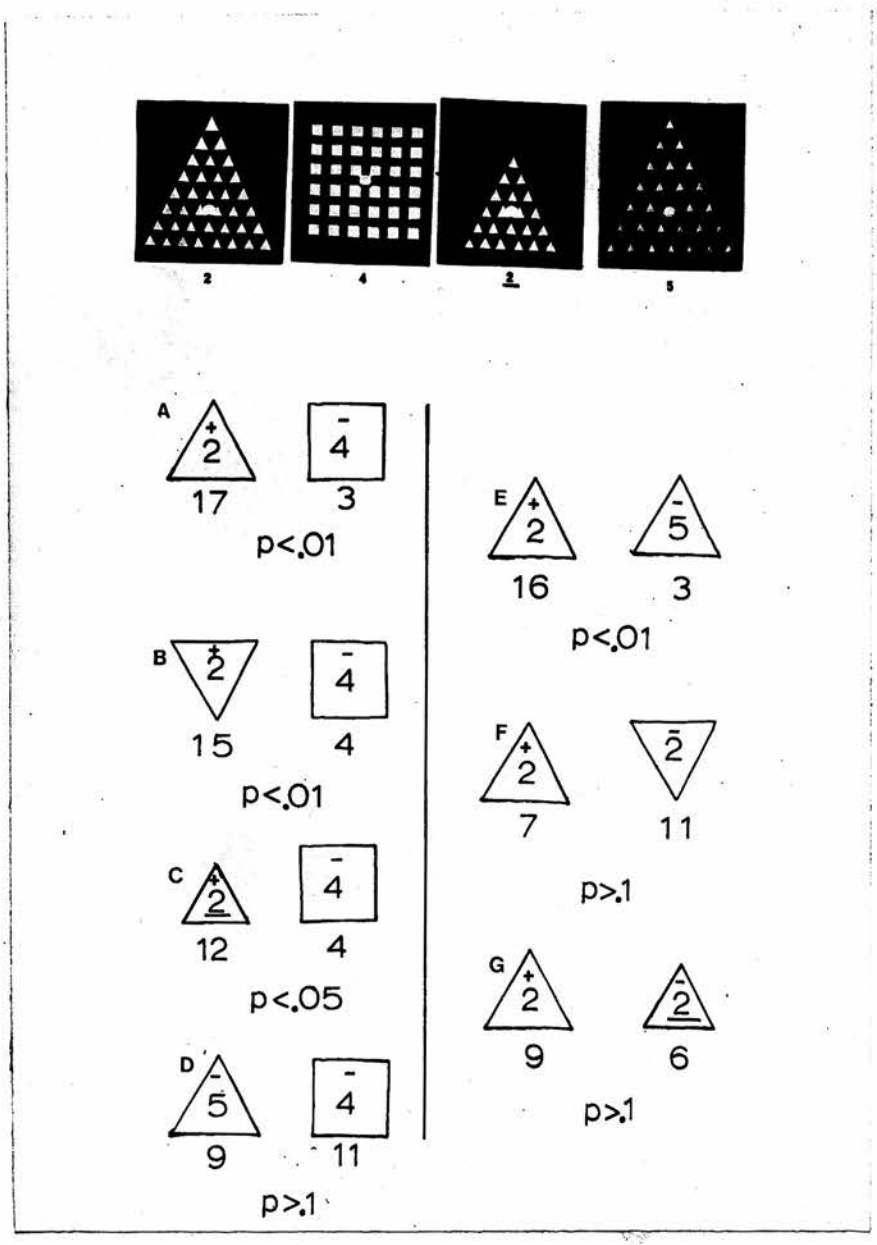
Apparatus

The training figures used in this experiment are shown at the top of figure thirty-six, each is seen as a bright figure against a black background. They were made by glueing a black cardboard 'stencil' of the shape onto yellow 'Day-Glow' paper so that the black cardboard frames a very bright figure. In each case the shapes were cut into rectangular cards of dimensions 10.7 x 12.2 cms. It can be seen that all the figures used are multiple ones, a triangle is composed of a set of small triangles and a square of a set of small squares. Mazochin-Porshnyakov always uses this type of figure and the shapes used in this experiment are designed to be similar to his.

Methods / .....

FIGURE THIRTY-SIX.

Training figures and results of experiment one.



Methods

A group of twenty bees was trained and tested on a series of figure pairs. The two members of a pair were laid out on a black table fifteen centimetres apart and at right angles to the line taken by the bees entering through the window. The shapes were covered by a sheet of glass and a clear plastic dish was placed above each of them. During training one of the shapes had the dish above it filled with two molar sugar solution while the dish above the other contained only water. Positions of the two shapes were interchanged every ten minutes to prevent the animals learning to respond to the position of reward. When this was done the glass plate covering the shapes was also wiped with alcohol and fresh dishes of sugar solution and water replaced the ones already in use. During testing neither shape carried reward and as each of the twenty bees entered the room its initial approach was noted i.e. the shape to which it first flew was recorded.

Results

The sequence of tests and the complete set of results is shown in figure thirty-six. The numbers inside the shapes show the shape number, these refer to the photographs of the actual shapes at the top of the figure. The numbers below the shapes show the number of initial approaches to each figure in a test situation. The training and testing sequence was performed as follows, the letters referring to the list of tests shown in figure thirty-six.

A) The group of twenty bees was trained on figures two and / .....

/ and four for thirty minutes, the triangle being rewarded. A test was then carried out and the results are shown. It was found that the bees had a distinct preference for the triangle. Training was then resumed on this discrimination for another thirty minutes.

B) After this training period, another test was carried out but with the triangle inverted. The bees still significantly preferred the triangle despite its change in orientation.

C) Another thirty minutes training was given on the original discrimination and then a test carried out with the triangle replaced by another of different size. Once more the bees significantly preferred the triangle although they had never seen this particular triangle before. Up to this point the experiment was very similar to the one performed by Mazochin-Porshnyakov, the size and orientation of the triangle have been successively altered but in each case the bees persisted in visiting the triangle.

D) The bees were again trained for thirty minutes on the original discrimination and then a test was carried out with the triangle replaced by one of different sub-unit size. The bees now chose randomly between the two figures, they showed no sign of generalising to this triangle. Mazochin-Porshnyakov did not ever find a triangle his bees did not generalise to, but sub-unit size remained constant throughout all his experiments.

E) Discrimination training was now carried out on the two / .....

/ two triangles of different sub-unit size. The original triangle, number two, was rewarded and the group of animals trained for thirty minutes. After this training a test was carried out and it can be seen that the group of bees discriminated these two figures.

F) The group of twenty bees was trained to discriminate the upright and the inverted triangle. The upright triangle was rewarded and the bees trained for thirty minutes. A test at the end of this period showed that the bees did not discriminate between these figures.

G) The bees were trained to discriminate the original training triangle and the triangle of reduced size. After thirty minutes training with the large triangle rewarded a test showed that the bees did not discriminate these figures either.

Conclusions

A group of honey bees were successfully trained to discriminate a multiple triangle from a multiple square. This discrimination persisted, just as Mazochin-Porshnyakov claimed, when the triangle was replaced by another triangle of different orientation or size. However, bees could not discriminate the triangles they had apparently 'generalised' to. Attempts to train the bees to tell apart either the large and small triangles or the triangles of different orientation failed. This suggests that the bees have not truly generalised to these figures but rather see them as being identical. Bees did not, however, generalise to a triangle of different sub-unit size and were able to tell this / .....

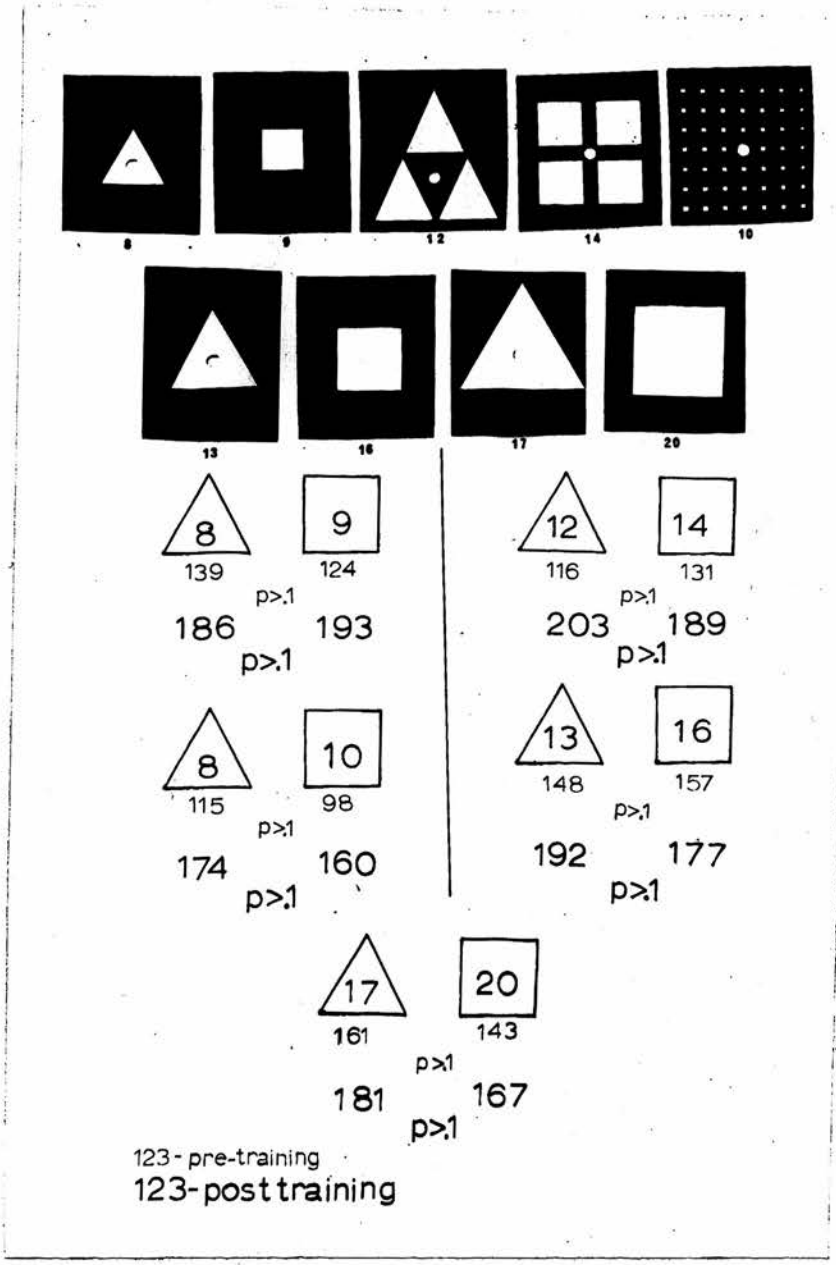
/ this triangle from the original training figure. Thus, the one triangle in thes experiment that bees could discriminate from the training triangle, was not treated as a 'triangle' in a generalisation test. These results do not support the conclusions of Mazochin-Porshnyakov that the bee 'generalises' and is capable of 'concept formation'. In two cases of apparent generalisation the bee was found unable to discriminate the training and transfer figures. The discrimination of the triangle from the square appears to be dependent upon factors which remain unchanged when the triangle is altered in size or orientation but which are dependent upon the sub-unit size or some parameter which changes when sub-unit size is changed. In the next experiment attempts are made to specify the parameters used by the bee in discriminating a triangle from a square.

Experiment two: The discrimination of triangles from squares was studied further. The methods were rather complicated as the experiment was designed both to analyse the parameters of form vision used by the bee and to test for complex generalisation processes of the type claimed by Mazochin-Porshnyakov. This second requirement limited this study to the discrimination of triangles and squares. An account was given of Sutherland's methodology in the introduction to this section on concept formation in the bee. The following experiments use similar methods.

Bees were trained on many pairs of triangles and squares in / .....

FIGURE THIRTY-SEVEN.

Training figures and results of experiment two.



/ in order to find out which shapes they could discriminate. Generalisation tests were then carried out to find what shapes the bees saw as similar. A major complication in discrimination tests is the existence of spontaneous preferences for certain shapes, a factor completely ignored by Mazochin-Porshnyakov. After discrimination training, if an animal shows no preference for either of the two figures this does not necessarily demonstrate that it cannot discriminate them. A pre-existing preference for the negative figure may have been modified so that the animal now sees both figures as equally attractive. The effect of training can only be judged by comparing preferences before and after it has taken place.

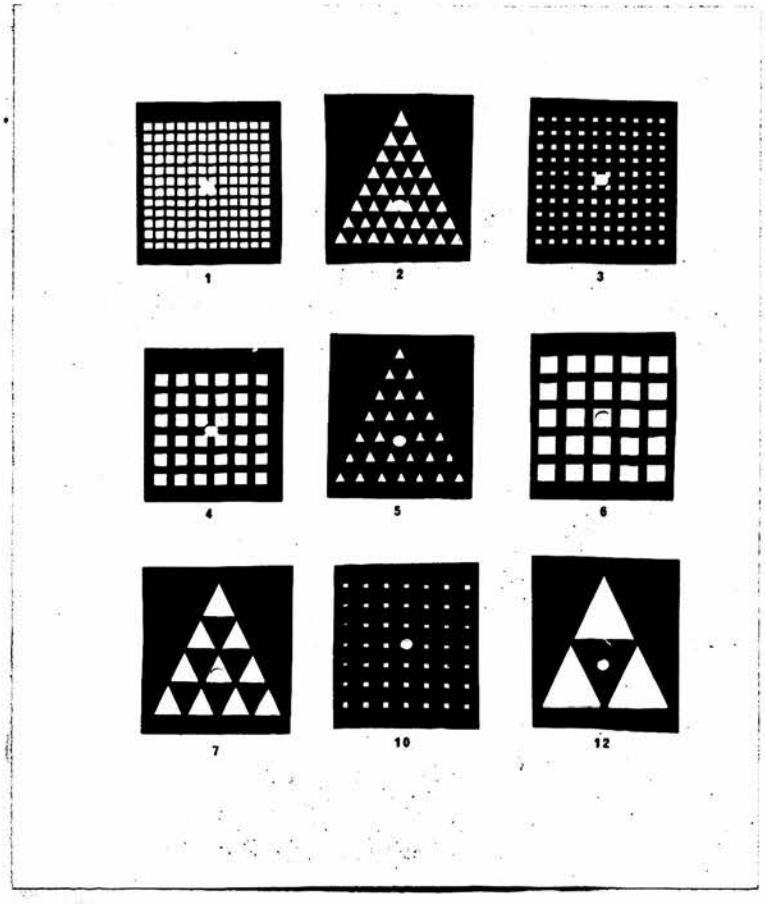
Spontaneous preferences also make generalisation tests much more complicated. If an animal is trained to discriminate two figures and then one is replaced by a transfer figure the preference for this new figure may give a measure of how similar it appears to the training figure. However, if this second figure is a highly attractive one the preference for it may be more a measure of how attractive it is than of its similarity to the training figure. The effect of generalisation can only be gauged by comparing the preference of bees for each of the transfer figures before and after training on the relevant discrimination.

Apparatus

The triangles and squares used in this experiment are shown in figures thirty-seven and thirty-eight. Once again they / .....

FIGURE THIRTY-EIGHT.

Training figures for Experiment two.



/ they are cut out of black cardboard and backed with yellow fluorescent paper.

Methods

The experiment was conducted with one pair of cards at a time laid out in the horizontal plane, as in the previous experiment. The training and testing procedures can be divided into three parts.

A) Pre-training choice test.

Firstly, the spontaneous preference for either the triangle or square of each pair was measured. Separate groups of twenty bees visited each pair of shapes seen in figure thirty-seven and listed in table seven. In each case both shapes in every pair were rewarded for one hour. At the end of this time an unrewarded approach test was carried out. In this test neither figure of the pair was rewarded and the total number of approaches made to each member of the pair was measured for a five minute period. By approach is meant a bee alighting on a card or flying up so close that its legs come within approximately one millimetre of touching the card. A similar scoring technique has already been dealt with in the preliminary experiments and gives a sensitive measure of the bees' preference. The number of approaches to each figure of each pair gives a measure of their relative attractiveness to the bee. The significance of the difference between the number of approaches to each figure of a pair was assessed with a chi-square test.

B) / .....

TABLE SIX.

Diagrammatic representation of methods.

\+ signifies reward. - signifies no reward.

Initial training.

Spontaneous preference tests.

Discrimination training.

Discrimination testing.

results compared with spontaneous preference.

Retraining.

Generalisation test.

results compared with spontaneous preference.

Retraining.

Generalisation test.

results compared with spontaneous preference.

/ B) Discrimination training and testing.

The triangle alone of each pair of figures shown in figure thirty-seven and in the training column of table seven now carried reward. Separate new groups of twenty bees visited each pair of figures for one hour. After this period of differential reinforcement a five minute unrewarded approach test was carried out with each pair of figures. If the training had not altered the apontaneous preference of the bees then training was resumed for a further period of three days. Another test was then carried out to see if this longer period of training had affected the bees choice behaviour. The significance of a change in choice behaviour was calculated by means of a chi-square test.

C) Generalisation tests.

For every pair of figures in which training had altered the preference of the bee, generalisation tests were carried out. Firstly, the bees were re-trained on the original discrimination for 30 minutes. The triangle was replaced by another which differed from it along a number of parameters and a five minute unrewarded choice test was carried out. The original training triangle was then replaced and the bees trained for a further thirty minutes with the triangle rewarded. Then the triangle was replaced by another triangle of different characteristics and a second unrewarded approach test carried out. The choice of the bees in these generalisation tests was compared with their spontaneous choices on an identical pair of figures. This made it possible to see if any preference for the triangle had been produced as / .....

/ as a result of training on a different triangle. A diagramatic representation of these methods is shown in table six.

Results

A) Pre-training tests. The pairs of shapes could be divided into two groups according to whether or not a spontaneous preference for either of the shapes existed. In all the pairs shown in figure thirty-seven (hereafter referred to as Group I), no significant preference for either shape existed. In all the pairs listed in table seven (Group II) there was a significant preference for either the triangle or square before training began.

B) Discrimination tests.

After one hour training a significant preference for the triangle existed in every pair of the shapes in Group II, the pairs that had spontaneously received different numbers of visits. In several cases the original preference for the square had been completely reversed.

After three days training none of the pairs in Group I showed a significant change in the proportions of visits to each figure.

Thus, only in those figure pairs in which spontaneous approach tests showed a preference for one or other of the figures did training cause the triangle to be significantly picked out.

C) Generalisation tests.

As shown in table seven, the discrimination of one triangle / .....

TABLE SEVEN.

The table opposite is divided into three pairs of columns. In the first column are shown the training fugures. Eight different pairs of training figures were used and they are numbered one to eight. For each pair of training figures is shown in the left hand column:-

a) the figure numbers, these refer to the photographs of the figures in figure thirty-eight.

b) the number of approaches in a spontaneous choice test and the probability(p1) from a chi-square test.

c) the number of approaches to each figure in a post training test and associated probability p2.

In the second two columns are shown the test figures, two generalisation tests were carried out for each training pair. In the two right hand columns are shown:-

a) the figure numbers.

b) the number of approaches to each shape in the pair in a spontaneous approach test.

c) the number of approaches to each figure in a generalisation test i.e. the number of approaches after bees have been trained on the training figures in the same row. The probability of a change from the previous spontaneous approach frequency is given as p3.

TABLE SEVEN.

		TRANSFER FIGURES.					
		Training figures.		test figures.		test figures.	
		△	□	△	□	△	□
1	Figure numbers.	2	1	5	1	7	1
	Spontaneous choice.	128	181	110	193	50	258
		p1 <.01					
	Post-training choice.	223	94	252	129	86	388
		p2 <.001		p3 >.1		p3 >.1	
2	Figure numbers.	5	4	2	4	7	4
	Spontaneous choice.	147	193	185	105	79	170
		p1 <.01					
	Post-training choice.	274	76	222	139	130	254
		p2 <.001		p3 >.1		p3 >.1	
3	Figure numbers.	7	6	5	6	8	6
	Spontaneous choice.	115	169	174	126	104	189
		p1 <.01					
	Post-training choice.	250	106	234	147	132	272
		p2 <001		p3 >.1		p3 >.1	
4	Figure numbers.	5	9	2	9	7	9
	Spontaneous choice.	203	93	288	49	208	115
		p1 <.001					
	Post-training choice.	342	17	329	68	226	153
		p2 <.001		p3 >.1		p3 >.1	
5	Figure numbers.	2	3	5	3	7	3
	Spontaneous choice.	179	141	188	116	91	259
		p <.05					
	Post-training choice.	372	40	234	153	88	304
		p <.001		p3 >.1		p3 >.1	

TABLE SEVEN continued.

		Training figures.		Test figures.		Test figures.	
		△	□	△	□	△	□
	Figure numbers.	2	4	5	4	7	4
6	Spontaneous choice.	185	105	147	193	123	226
		p1<.001					
	Post-training choice.	344	47	192	224	116	249
		p2<.001		p3>.1		p3>.1	
7	Figure numbers.	8	16	7	16	12	16
	Spontaneous choice.	202	135	209	96	157	145
		p1<.001					
	Post-training choice.	268	102	251	126	201	172
		p2<.001		p3>.1		p3>.1	
8	Figure numbers.	5	10	7	10	2	10
	Spontaneous choice.	249	76	164	135	241	72
		p1<.001					
	Post-training choice.	318	33	218	160	309	68
		p2<.001		p3>.1		p3>.1	

/ triangle from a square never affected the preference of the bees when the triangle was replaced by a different one. In no case did bees generalise from one triangle to another.

Conclusions

The effect of differential reinforcement training appears to be only to modify pre-existing preferences. Figure pairs which received an equal number of visits in a spontaneous choice test continued to do so after three days training with only the triangle rewarded. Figure pairs which received an unequal number of visits in a spontaneous choice test had their preferences significantly modified by a period of training. In the cases where the bee did learn to pick out the triangle, this preference was not generalised to any of the other triangles. No evidence was found for any generalisation which would require us to postulate the formation of a concept of 'triangularity'. In every case the discrimination was specific to the particular pair of figures involved.

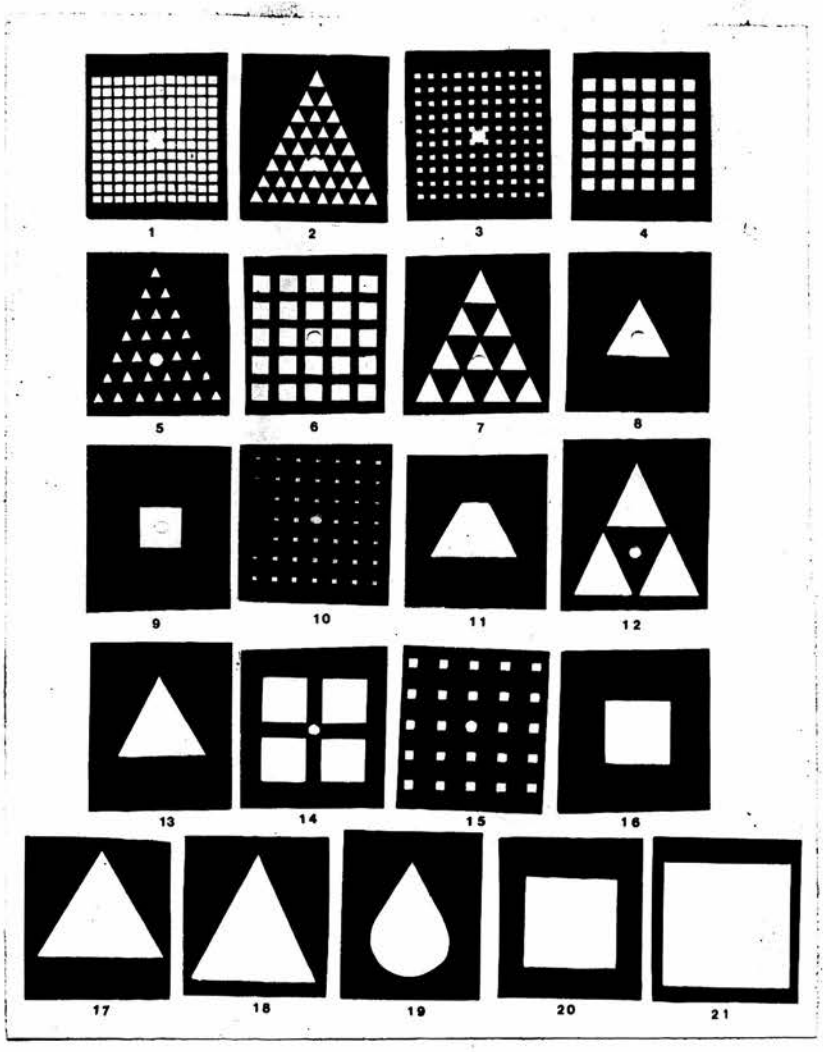
The correlation between changes in preference as a result of training and the existence of a spontaneous preference suggests that the parameters which determine the spontaneous attractivity of shapes are the same parameters used by the bee in discriminating shapes. In the next experiment the factors determining spontaneous attractivity are examined in more detail. After this experiment is described a more detailed examination of the results above is carried out.

Experiment three: The spontaneous attractivity of shapes.

In / .....

FIGURE THIRTY-NINE.

The complete set of training figures.



/ In this experiment the relative attractiveness of a large number of shapes was assessed.

Apparatus

A large number of different triangles and squares were used in this experiment; the complete set is shown in figure thirty-nine. All the shapes were cut out of standard sized rectangles of black cardboard and backed with yellow fluorescent paper.

Method

The shapes were all presented horizontally on a large black table. They were covered with a sheet of glass and above every shape was placed a dish of two molar sucrose solution. A group of sixty bees was allowed to visit the array of shapes for one hour. Then for a period of ninety minutes the number of bees landing on each figure was recorded. Every ten minutes the positions of the shapes were randomly interchanged. At the same time the glass plate covering them was wiped with alcohol and the dishes of sugar solution exchanged for clean ones.

Results

The number of visits made to each figure listed in the same order as figure thirty-nine is shown in the extreme right hand column of table eight. The characteristics of all the shapes along a number of different parameters are also presented in table eight.

These are:

1) The figural intensity; the number of centimetres of dark/light / .....

TABLE EIGHT.

PARAMETERS OF THE TRIANGLES AND SQUARES.

Figure number	Figural intensity cms/sq.cm	Figure area sq.cms	Total Sub-unit area sq.cms	Sub-unit intensity cms/sq.cm	Number of sub-units
1	4.5	90	71	5.7	144
2	2.7	48	22	6.0	36
3	2.2	90	25	8.0	100
4	2.0	72	36	4.0	36
5	1.8	49	11	7.7	28
6	1.7	90	56	2.7	25
7	1.5	48	26	2.7	10
8	1.4	11	11	1.4	1
9	1.2	11	11	1.2	1
10	1.1	90	12	8.0	49
11	1.0	19	19	1.0	1
12	1.0	47	32	1.4	3
13	0.9	22	22	0.9	1
14	0.9	64	49	1.1	4
15	0.8	99	16	5.0	25
16	0.8	25	25	0.8	1
17	0.7	42	42	0.7	1
18	0.7	47	47	0.7	1
19	0.6	34	34	0.6	1
20	0.6	49	49	0.6	1
21	0.4	88	88	0.4	1

TABLE EIGHT continued.

Figure number	Contour length cms	Single Sub-unit area sq.cms	Area ratio.	No. of visits
1	405	0.5	0.8	674
2	129	1.3	0.5	535
3	198	0.9	0.3	456
4	144	2.0	0.5	377
5	88	1.7	0.2	312
6	153	3.6	0.6	233
7	72	4.8	0.5	156
8	15	11.0	1.0	109
9	13	11.0	1.0	94
10	99	1.8	0.1	108
11	19	19.0	1.0	72
12	47	16.0	0.7	52
13	20	22.0	1.0	73
14	58	16.0	0.8	64
15	79	4.0	0.2	52
16	20	25.0	1.0	64
17	29	42.0	1.0	44
18	33	47.0	1.0	61
19	20	34.0	1.0	48
20	29	49.0	1.0	57
21	35	88.0	1.0	62

/ dark/light contour per unit area of the shape.

2) The figure area; the area of the figure as we would view it as a triangle or a square.

3) The total sub-unit area; the total area of the light parts of the figure.

4) The sub-unit intensity; the number of centimetres of dark/light contour per unit area of each little sub-unit.

5) The number of sub-units; the total number of sub-units in a shape.

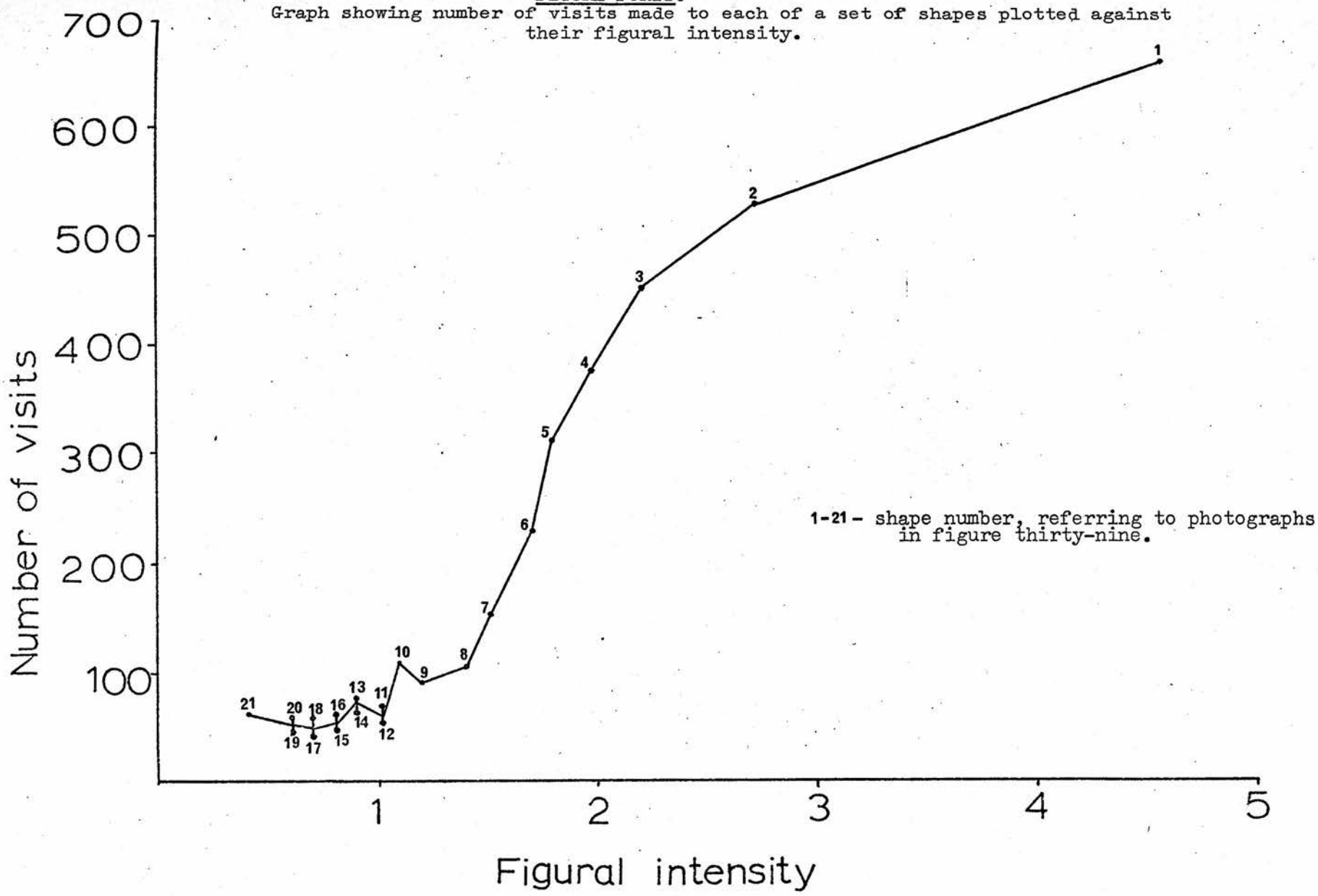
6) The contour length; the total length of dark/light contour in a shape.

7) The single sub-unit area; the area of each individual sub-unit.

8) The area ratio; score two divided by score seven, an index of the amount of figure that is light.

Finally, the number of visits received by the shapes is shown. The number of visits, an index of the attractiveness of the shapes to the bee, correlates extremely well with the figural intensities of the shapes. It does not correlate with any other stimulus parameter reported here. The relationship between figural intensity and number of visits is displayed graphically in figure forty. Plotted here is the total number of approaches to each shape against figural intensity. The shape numbers are also shown along the X-axis in / .....

FIGURE FORTY.
Graph showing number of visits made to each of a set of shapes plotted against their figural intensity.



1-21 - shape number, referring to photographs in figure thirty-nine.

/ in positions according to their figural intensities. Shapes of low figural intensity (between 0.4 and 1.0) received a similar low number of visits. No significant difference existed in the number of visits received by these shapes. The curve can be seen to rise steeply from a figural intensity value of 1.4, the higher the figural intensity of these shapes the more visits they received.

Conclusions

In a spontaneous choice situation in which there was no differential reinforcement bees were attracted to shapes according to their figural intensities. Within the limits of the experiment described, the higher the figural intensity of a shape the more attractive it was to the bee. Shapes of low figural intensity were equally unattractive to the bee. Although they approach the phenomenon from a rather different angle, these results are in complete agreement with those of Zerrahn (1933) described in the introduction to this section on concept formation.

The results of the previous experiment suggested that the bees can be trained to discriminate shapes only if there are initially differences in their spontaneous attractivity. This experiment suggests that the spontaneous attractivity of figures is dependent upon their figural intensities. Is it possible to explain all the discriminations performed by the bee in the previous experiment on the assumption that figural intensity is the only parameter of shape abstracted by the bee ? It is now postulated that bees can be trained to / .....

/ to discriminate shapes only if they have detectable differences in figural intensity. Shapes with identical figural intensities are postulated to be identical for the bee. It is assumed that among shapes of low figural intensity, the shapes lying on the initial flat portion of the graph shown in figure forty, differences in figural intensity cannot be detected. All these shapes receive an equal number of visits in the spontaneous preference test. Returning to the previous experiment:

a) The shapes which the bees could not be trained to tell apart (figure thirty-seven) are all of low figural intensity and fall outside the range of values in which differences in figural intensity are assumed to be detectable.

b) All the shapes which bees could be trained to discriminate (Table seven) have figural intensity values in the range in which differences can be detected.

c) The bees never generalised to other triangles. All the transfer triangles have values of figural intensity different from the training triangles and thus would not be seen as being similar.

No other parameter appeared to explain the pattern of results found in the previous experiment. Other parameters might be tested in the following manner. Looking at the first discrimination in table seven, triangle two is discriminated from square one. If it was postulated that the bee detects differences in form only on the basis of differences in area this discrimination would be predicted as / .....

/ as these two shapes are different in area. However, bees do not generalise to shapes five or seven although they have the same area as shape two and on an area parameter are identical to this shape. An area parameter alone would thus be ruled out as a satisfactory explanation. Carrying out this kind of logical process it is found that only by assuming that bees detect and respond to differences in figural intensity can all the discriminations performed in these experiments, and also those described by Mazochin-Porshnyakov, be explained. In his experiments all his triangles and all his squares, whatever their colour, size, orientation, etc. had a constant sub-unit size. Thus all his triangles had one value of figural intensity and all his squares had a different constant value. Consequently, all his experiments may be explained by the assumption that the bees were simply responding to the constant figural intensity differences between the set of triangles and the set of squares. Despite the many changes he makes in his shapes, differences on this one parameter remain unchanged throughout the experiment. In conclusion, it is possible to discount his claims of 'generalisation' and 'concept formation' and re-affirm early theories which suggested that the parameter of figural intensity is abstracted by the bee and differences in this parameter serve to discriminate shapes.

Experiment four: The last three experiments suggest that the parameter of figural intensity is abstracted by the bees form vision system. However, there are clearly examples of discriminations by bees in which figural intensity plays little part. Wehner (1970) has been able to show that bees can / .....

/ can be trained to tell apart stripes of different orientation displayed on a vertical screen. The stripes are identical except for their orientation and clearly no differences in figural intensity exist. In the experiment to be described below an attempt is made to force bees to use parameters other than figural intensity in discriminating triangles from squares. It is possible that figural intensity is only one parameter in a hierarchy of potential abstraction mechanisms and that others can be made to operate given the right conditions.

It was shown in the previous experiment that bees could not discriminate simple shapes of low figural intensity. Even after three days training on a discrimination of a triangle and square of low figural intensity no preference for the triangle could be found. In the experiment to follow bees are trained over a long series of discriminations. Training commences with pairs of figures both of high figural intensity and then proceeds through a series of pairs of progressively lower figural intensity. Eventually, the pairs of simple shapes are reached which were previously found to be indistinguishable. It was hoped that by gradually reducing figural intensity over a series of discriminations, it would become gradually more and more difficult for the bees to use differences in figural intensity. Levels of figural intensity would be approached which have been found to be indiscriminable by the bee. As it became more difficult for the bee to / .....

TABLE NINE.

TRAINING THROUGH A LONG SERIES OF FIGURE PAIRS.

Series of training pairs.
Triangle v. Square.
1. 2 v 1
2. 2 v 3
3. 2 v 4
4. 2 v 6
TEST ONE.
5. 5 v 1
6. 5 v 3
7. 5 v 4
8. 5 v 6
9. 5 v 9
TEST TWO.
10. 7 v 1
11. 7 v 3
12. 7 v 4
13. 7 v 6
14. 7 v 9
15. 7 v 10
TEST THREE.
16. 8 v 1
17. 8 v 3
18. 8 v 4
19. 8 v 6
20. 8 v 10
TEST FOUR.
21. 12 v 4
22. 12 v 6
23. 12 v 9
24. 12 v 10
25. 12 v 14
26. 12 v 15
27. 12 v 16
TEST FIVE.
28. 13 v 4
29. 13 v 6
30. 13 v 9
31. 13 v 10
32. 13 v 14
33. 13 v 15
TEST SIX.

Series of tests.			
	Number of approaches to each figure of the test pair.		P-value from chi^2 test.
	Triangle no. 13.	Square no. 16.	
TEST 1	181	168	>.5
" 2	213	196	>.5
" 3	228	183	<.05
" 4	174	139	<.05
" 5	226	177	<.02
" 6	201	142	<.001

/ to respond to differences in figural intensity it was hoped that other parameter systems would be brought into operation.

Apparatus

The vertical plane training a pparatus described in the general methods section was used. The training figures are identical to those used in the previous experiment and are all shown in figure thirty-nine.

Methods

A group of twenty bees was trained over a series of discriminations between triangles and squares, the full list of discriminations is shown in table nine. It can be seen that training began with figure pairs of high figural intensity and gradually passed to figure pairs of low figural intensity. In each case the triangle of the pair was rewarded and training continued for thirty minutes. At intervals, a test was carried out. During each test, triangle number thirteen and square number sixteen, were placed on the vertical board and the total number of approaches to each shape recorded over a five minute period. Neither shape was rewarded during a test. It has already been shown that the bees had no spontaneous preference for either figure of this test pair and could not under the conditions previously used, be trained to discriminate them.

Results

The results are also shown in table nine. The number of approaches made to each shape during each test is shown in the right hand column.

On the first two tests the bees showed no preference for / .....

/ for the triangle of the pair of simple shapes. However, by the third test a slight preference for the triangle emerged and by the sixth test a highly significant preference for the triangle was seen.

Conclusions

By training through a whole series of triangles and squares of decreasing figural intensity a discrimination of a simple triangle and square emerged. By the time a significant discrimination was observed bees had received training on a series of thirty-three pairs of triangles and squares over a period of three days. Previously, three days direct training on the discrimination of this same triangle and square had failed to have a significant effect. In the next experiment the parameters used by the bee in this discrimination are investigated. It is possible that the bee is still responding to differences in figural intensity because training through a series of figures may have increased the sensitivity of the bee to differences between low values of

Experiment five: An attempt was now made to find out what parameters are used by the bees in discriminating a simple triangle from a simple square.

Methods

Exactly the same training procedure was used as in the previous experiment except that the intermittent tests were not carried out. When the discrimination of triangle thirteen from square sixteen had become established as a result of three / .....

FIGURE FORTY-ONE.

Final series of generalisation tests.

three days training the bees were given a series of generalisation tests. Before each of such tests, triangle thirteen was placed alone in the central position of the vertical training apparatus and rewarded for ap period of thirty minutes. During tests this triangle was removed and a triangle and square placed at positions equidistant from the central training position. Neither shape was rewarded and the total number of appraoches made to each figure was recorded over a five minute period. The full series of tests is shown in figure forty-one. As usual, the number inside the shape shows the figure number and refers to the photographs of the shapes at the top of the figure. The numbers beneath the shapes show the total number of approaches to each figure. The test sequence was carried out three times with three groups of twenty bees. The first two times tests A to H were carried out and in the final run, tests A to N. In each case testing was stopped not at the time desired by the experimenter but at the time dictated by the weather. The figures shown beneath the shapes represent the total number of approaches from all the tests so that the figures shown for tests A to H are the totals of three repeats. The significance of differences in the number of approaches to each of the figures of a pair was assessed by means of a chi-square test.

Results

All the generalisation tests are shown in figure forty-one and they are discussed in the order shown in the diagram.

A) The bees discriminate triangle thirteen from square sixteen.

B) / .....

/ B) The triangle and square were replaced by another pair of smaller size and the triangle was still significantly preferred.

C) The bees were tested on a larger pair of figures and still preferred the triangle.

D) The orientation of triangle thirteen was changed and the bees ceased to have any significant preference for the triangle.

E) and F) Tests B and C were repeated with the triangles inverted and in each case no preference for the triangle was seen.

G) and H) To check that the failure of the bees to pick out the inverted triangle in the last three tests was not due to their having lost the ability to discriminate an upright triangle from a square, tests B and C were repeated. In each case the bees still significantly preferred the triangle.

I) and J) The base of the triangle was altered by rounding it out and two tests carried out in conjunction with squares of different areas. In both cases the bees significantly preferred the distorted triangle.

K) and L) The triangle was changed in another way by blacking out its apex. Two tests were carried out with squares of different areas but in neither case did the bees show a significant preference for the 'triangle'.

M) and N) Once again discrimination tests B and C were repeated / .....

/ repeated to check that the failure of the bee to pick out the 'triangle' on the last two tests was not due to a complete failure of the ability of the bee to discriminate the simple triangle and square. In both tests the upright triangle was significantly preferred.

Thus, in a series of discriminations bees discriminated simple triangles from squares in spite of changes in size or distortions in the base of the figure. However, if the triangle was inverted or its apex was 'cut off' bees cease to have any preference for the 'triangle'. In all the tests in which the bees preferred the triangle, the top part of the figure was an acute angle while in every case where discrimination failed this feature was absent. Clearly, these results are not explicable on the basis of differences in a figural intensity parameter. Neither can these results be explained on the basis of the only other parameter that bees are thought to abstract. In the final part of the experiment bees generalised to figures which were very different in their distribution of areas being respectively black and white and did not generalise to figures which were a much closer fit in these terms. It appears that bees can respond to some other parameters of shape under the right circumstances, possibly to the presence of an acute angle in a particular area of the figure.

In the introduction to this section on concept formation in the bee an experiment was mentioned, and is shown in figure thirty-three, which as yet defies explanation. It is interesting to note that there are similarities between this and the final one reported here. When the ends of the arms of the / .....

/ the shapes A, B and D in figure thirty-three are blunt the bees accept them as being similar. When the ends of the arms are then made pointed, as in shape C, the bees refuse to visit the shape. It may be that the bee can discriminate acute angles in a shape as both this discrimination and the one reported here could be explained on this basis. The true nature of the processes underlying the ability of the bee in these experiments can only, as yet, be the subject of speculation.

Conclusions

Reviewing this section on the discrimination of shape by the honey bee, several conclusions may be drawn.

Firstly, it may be concluded that the claim made by Mazochin-Porshnyakov, that the discrimination of triangles from squares by the bee makes it necessary to postulate that bees are capable of concept formation, is incorrect. Rather, it appears that in this situation bees abstract the parameter of figural intensity and differences on this one parameter alone will account for all the discriminations studied by Mazochin-Porshnyakov and all those reported here in analagous for many years.

Secondly, as a result of special training procedures, discriminations were performed by the bee not explicable on the basis of differences in figural intensity. Although the mechanisms underlying these discriminations are not understood it seems possible that bees can abstract information about angles.

Although / .....

Although attempts to find examples of concept formation in the bee have not proved successful, the most important parameter the bee appears to use, that of figural intensity, appears well adapted to its needs. Beds of flowers or masses of blossom on a tree will provide forms of high figural intensity which are easily discriminated by the bee. As it has a preference for figures of high figural intensity it will automatically pick out floral forms in its natural environment. The research reported here shows that bees can easily discriminate figures of different high figural intensity and presumable bees can learn to visit flowers of different species on this basis. The preference for high figural intensity shapes will not help it find its way back to the hive, the entrance of which will be a large simple shape. However, there is some evidence that the preference of bees for high figural intensity shapes is reversed when it has fed and is returning to the hive (von Frisch 1969). If this is correct then the whole ability of the bee to discriminate shapes may differ according to whether it is looking for food or for the hive. This system should be a fascinating topic for further research.

CONCLUSIONS.

A considerable proportion of the introduction was devoted to discussion of comparative studies of learning and of attempts to relate these studies to the 'evolution of learning'. The experiments described in this thesis enable some criticism of this approach to be made.

Two experiments with conventional reversal learning tasks have been described, one with the cockroach and one with the honey-bee. In common with all 'lower' animals that have been studied, neither animal showed improvement over a series of reversals as a function of reversal experience. Cockroaches showed a pattern of changes in error elimination similar to that seen in several other species which fail to improve over a series of reversals. In contrast, the changes seen in bees over a series of reversals appears unique to that species. Deterioration in performance has been observed occasionally in both fish (Warren 1960c) and chickens (Mackintosh 1965) but in each case appears to be due to the animal continuing to respond to the previously correct cue after a reversal. The bee shows a quite different pattern of changes in error elimination over a series of reversals. On late reversals, the bee stops responding to the previously correct cue almost immediately but then, for a long period, visits both cues equally often. This pattern of behaviour would not be predicted by either attentional or pro-active inhibition theories of reversal learning. The bee appears to fall into a seperate category from other animals that have been studied in this situation.

Other / .....

/ Other recent work suggests that similarities between the reversal learning behaviour of different species may have been overstressed. Originally, Bitterman proposed that animals might be divided into two categories simply on the basis of whether or not they showed improvement in a reversal learning situation. He considered that this difference corresponded to a fundamental dichotomy in the learning processes of the animals concerned and that his experiments thus mapped out the emergence of qualitatively new learning capabilities - 'the evolution of intelligence' (Bitterman 1960, 1963, 1965). However, other evidence showed that even 'lower' animals might show some improvement on a reversal learning task and that differences between animals were of degree rather than of kind (Mackintosh 1969, Mackintosh et al 1971, Mackintosh & Canty 1971). In many of the early studies of reversal learning comparisons were made only on the basis of differences between errors to criterion on early and late reversals. When the error patterns of animals have been studied in more detail a great diversity of behaviour emerges (e.g. Bitterman 1971; Mackintosh & Little 1969). Although some unitary scheme may unite the results from different species it now seems likely that the changes in behaviour seen in reversal learning are themselves diverse and the result of highly complex phenomena.

In comparative studies of reversal and other learning tasks there has been a commom belief that the tests can be related to a single quality of 'intelligence'. This belief stems from the view of many psychologists that learning in

all/.....

all animals is fundamentally the same, different animals differing only in capacity. Until recently, Bitterman was one of the few learning theorists who believed that there might be more than one 'kind' of learning, but even he thought in terms of a linear scale in which new abilities were 'added' as the phylogenetic scale was ascended (Hodos and Campbell 1969). The point was made in the introduction that certain animals seemed to have specialised learning capabilities, this would suggest that rather than each lying at some point on a linear scale which plotted 'learning ability', every species should be considered only in relation to its own environment. Experiments reported in this thesis support this conclusion.

Bees were shown to be unable to decide which of two cues to visit when this was determined by a second colour cue but they are known to be able to solve this same problem easily when reward is dependent upon a time cue.

Learning is essentially a process of adaptation to a changing environment, in any particular environment some problems are going to be met much more frequently than others. We might even expect animals from different phyla to show similar learning capabilities if they are faced with similar problems in their natural life. For example, a honey-bee and a humming-bird both rely upon the secretions of flowers as a source of food. It is quite possible that the humming-bird would also show a particular capability for dealing with time-dependent cues. However, as the two animals have quite different nervous systems we would expect similarity only in some respects.

Another / .....

/ Another specialisation might be considered present in the remarkable ease with which cockroaches could learn avoidance of an area in which they had been punished. Maier (1970) points out a number of similar examples "Arthropods such as jumping spiders that prey on insects - and presumably benefit from identification of unpalatable prey - learn avoidance responses very quickly (Drees 1952); these avoidance responses are learned more readily than comparable approach responses. On the other hand, many ants have difficulty with avoidance learning, but learn approach responses relatively quickly; these approach responses are presumably related to an ability to locate the nest". It might be added that the praying mantis also shows a remarkable avoidance learning ability (Gelperin 1968). This avoidance learning is 'passive', the animal learns not to strike at prey objects which have been found to be unpleasant. Such a capability might be expected of a predator, cockroaches on the other hand seem especially adapted to learn 'active' avoidance responses, they learn to run from an area in which they have been 'attacked'. The importance of avoidance learning in the life of the cockroach was pointed out in the experiments conducted in the semi-natural situation.

Earlier in this thesis some experiments were described (Mazochin-Porshnyakov 1969) which suggested that bees possessed a remarkable ability for visual concept formation, possibly an ability comparable with that seen in higher mammals. It was thought that this ability might be / .....

be related to the remarkable orientation and flower foraging habits of the bee. The series of experiments that investigated visual discrimination in the bee found, in fact, that animals relied largely upon the parameter of figural intensity for shape discrimination. Although bees do not have the remarkable ability that had been attributed to them, the parameter they abstract is beautifully adapted to their needs.

As a final point, the major and almost inevitable defect of a thesis of this type should be indicated. In trying to tackle general questions a series of partially unrelated specific experiments have to be performed. The problems raised in the introduction can only really be answered by a great array of experiments drawn from the work of both comparative psychologists and ethologists, and not by a few experiments on a couple of species.

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APPENDICES.

APPENDIX 1

PRELIMINARY EXPERIMENTS

A. LEARNING IN A T-MAZE WITH DARK REWARD

Distance Run in Inches

Animal Number \ Trial Number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1	6	18	6	6	8	6	6	R	6	18	14	6	R	6	6	6	6
2	14	25	6	14	6	12	18	6	28	8	R	6	R	6	6	6	6
3	R	14	6	6	6	R	R	R	6	6	6	6	R	6	6	R	6
4	26	14	6	14	6	6	6	6	6	14	6	14	6	14	6	6	6
5	R	6	14	R	14	R	6	6	R	R	14	26	6	6	R	14	R
6	6	14	6	16	6	14	6	6	6	6	6	6	14	R	6	14	6
7	14	6	6	12	6	6	14	R	6	6	6	14	R	14	6	6	6
8	14	18	14	6	12	R	R	14	6	6	6	6	6	6	6	6	14
9	6	6	36	6	6	6	14	6	16	6	6	R	14	6	6	6	6
10	14	6	6	6	18	R	6	6	6	14	6	6	6	6	R	6	14
Mean Distances Run	12.5	12.7	10.6	8.4	8.8	8.3	9.5	6.6	8.9	9.3	7.8	10.0	8.6	8.7	6.0	7.8	7.8

APPENDIX 1 (Cont'd)

PRELIMINARY EXPERIMENTS

A. LEARNING IN A T-MAZE WITH DARK REWARD (Cont'd)

Distance Run in Inches

Animal Number / Trial Number	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
1	6	R	6	6	6	6	6									
2	6	6	14	6	6	6	6									
3	6	6	6													
4	6	6	6	6	6	6										
5	6	6	6	R	R	14	16	14	R	R	14	6	6	R	R	R
6	6	6	6	6	6	6	14	6	6							
7	14	6	14	6	6	6	6	6	6	6	6	6				
8	6															
9	14	6	6	6	14	14	14	6	6	6	6	6	6	6	6	6
10	6	6	6	14	6	6	6	6	6	6						
Mean Distances Run	7.6	6.0	7.8	7.1	7.1	7.1	8.3	7.6	6.0	6.0	8.7	6.0	6.0	6.0	6.0	6.0

APPENDIX 1 (Cont'd)

C. LIGHT INTENSITY AND AVOIDANCE

Average Amount of Time Spent in the Dark by a Group of 5 Animals in each Five Minute Period (in Minutes and Seconds)

Light Intensity in Foot-Candles	Five Minute Periods 1	2	3	4	5	6	7	8	9	10	11	12
1.5	0.20	0.10	1.10	1.50	2.10	3.20	4.00	3.45	4.00	4.00	3.70	3.40
5	0.55	1.15	1.55	2.45	2.50	3.30	3.45	4.15	4.35	4.10	3.40	4.05
10	2.05	2.30	2.20	2.55	3.15	3.55	4.10	4.20	4.20	4.15	4.00	3.00
16	3.45	3.35	4.05	4.25	4.50	5.00	4.45	5.00	4.50	4.30	3.50	3.20
20	4.25	3.00	4.40	4.55	3.00	4.45	3.00	4.35	4.20	4.45	4.25	3.15
24	5.00	5.00	5.00	5.00	5.00	4.05	5.00	4.50	4.85	4.75	4.20	4.30

APPENDIX 2

FOOD DEPRIVATION EXPERIMENTS

Days Deprived	Seconds Reward/ Trial	Number of trials/day	MEAN NUMBER OF ERRORS IN GROUPS OF FIVE ANIMALS OVER BLOCKS OF FIVE TRIALS									
			TRIALS IN GROUPS OF FIVE									
			1-5	5-10	10-15	15-20	20-25	25-30	30-35	35-40	40-45	45-50
14 days	0.25	2	2.4	2.9	1.7	2.6	1.9	3.5	2.0	3.0	2.4	2.3
		5	2.6	1.9	2.1	1.4	2.7	1.9	2.2	3.3	2.0	2.5
		10	2.3	2.8	2.7	1.9	2.5	2.1	3.4	2.5	2.5	2.3
	1	2	3.1	1.9	3.0	1.8	2.1	2.5	1.7	2.9	3.5	2.1
		5	2.5	2.8	2.6	2.8	2.5	2.7	2.3	2.3	2.8	2.0
		10	2.5	1.8	2.2	2.5	1.7	2.3	1.5	3.3	2.8	1.9
	5	2	2.5	1.8	2.3	2.5	2.1	3.3	2.3	2.4	1.8	2.7
21 days	0.25	2	2.8	1.5	2.8	2.9	1.8	2.1	2.5	2.5	2.5	3.0
		5	2.9	2.9	2.3	2.5	2.1	2.5	2.8	1.7	2.5	2.4
		10	2.6	1.9	1.3	2.7	1.9	2.8	3.4	2.0	2.5	2.3
	1	2	2.4	2.2	2.1	3.5	1.9	2.8	2.3	1.6	2.9	2.5
		5	2.7	2.1	2.6	2.3	2.0	2.3	2.1	2.9	1.4	2.5
		10	2.5	2.4	1.9	2.3	1.8	3.4	2.0	2.5	2.9	2.3

A P P E N D I X 2 (Cont'd)

FOOD DEPRIVATION EXPERIMENTS (Cont'd)

Days Deprived	Seconds Reward/ Trial	Number of Trials/Day	MEAN NUMBER OF ERRORS IN GROUPS OF FIVE ANIMALS OVER BLOCKS OF FIVE TRIALS									
			TRIALS IN GROUPS OF FIVE									
			1-5	5-10	10-15	15-20	20-25	25-30	30-35	35-40	40-45	45-50
21 days	5	2	2.3	2.3	2.4	2.5	2.9	1.7	3.5	1.7	2.5	3.4
		5	2.4	1.8	2.3	2.5	2.7	1.9	2.0	2.7	3.4	2.8
35 days	0.25	2	2.4	2.2	2.0	3.0	1.7	2.1	2.8	2.2	2.9	2.3
		5	2.5	2.8	1.7	3.1	2.7	2.2	2.2	1.8	2.3	2.2
		10	2.5	1.5	2.9	2.2	1.9	3.3	2.3	1.7	2.3	3.0
	1	2	2.7	2.5	1.5	2.6	2.5	3.8	2.3	2.1	2.4	1.8
		5	2.4	2.7	2.5	2.1	2.8	1.7	2.7	1.9	2.7	2.9
		10	1.7	2.4	1.8	2.2	2.9	1.8	2.4	2.7	2.5	2.6
	5	2	2.4	2.0	3.3	2.3	2.1	2.1	2.6	2.9	1.4	2.0
		5	2.5	1.8	2.4	1.7	2.5	1.9	2.1	2.6	3.1	2.1

APPENDIX 2 (Cont'd)

FOOD DEPRIVATION EXPERIMENTS (Cont'd)

Days Deprived	Seconds Reward/ Trial	Number of Trials/Day	MEAN NUMBER OF ERRORS IN GROUPS OF FIVE ANIMALS OVER BLOCKS OF FIVE TRIALS									
			TRIALS IN GROUPS OF FIVE									
			50-55	55-60	60-65	65-70	70-75	75-80	80-85	85-90	90-95	95-100
14 days	0.25	2	2.5	2.1	1.8	2.9	2.1	2.3	2.8	2.4	2.9	2.5
		5	2.8	1.6	2.1	3.3	2.7	2.7	1.9	2.9	2.1	2.7
		10	2.8	2.0	2.6	2.3	2.4	2.7	3.2	2.9	2.5	2.7
	1	2	2.3	2.5	2.0	2.7	2.1	3.1	2.5	2.7	2.1	2.9
		5	1.9	2.9	1.9	2.7	2.7	3.0	2.3	2.75	2.3	2.3
		10	3.0	2.5	2.2	2.7	2.2	3.4	2.6	2.3	2.4	2.5
	5	2	2.5	3.1	2.5	3.1	2.8	1.2	2.1	3.3	2.9	2.5
21 days	0.25	2	3.0	2.0	2.7	2.1	2.7	3.0	2.0	2.4	2.3	2.5
		5	3.0	2.5	2.3	3.4	2.7	2.8	2.2	3.1	2.9	2.3
		10	3.5	2.5	2.3	2.5	2.1	2.9	3.6	2.5	2.9	2.0
	1	2	3.0	2.2	2.5	3.0	3.0	1.9	2.7	2.6	2.7	2.4
		5	3.5	1.7	2.8	2.0	2.3	2.5	1.8	2.5	3.2	2.4
		10	2.5	2,1	2.9	2.9	1.9	3.0	2.5	2.3	2.9	2.1

APPENDIX 2 (Cont'd)

FOOD DEPRIVATION EXPERIMENTS (Cont'd)

Days Deprived	Seconds Reward/ Trial	Number of Trials/Day	MEAN NUMBER OF ERRORS IN GROUPS OF FIVE ANIMALS OVER BLOCKS OF FIVE TRIALS									
			TRIALS IN GROUPS OF FIVE									
			50-55	55-60	60-65	65-70	70-75	75-80	80-85	85-90	90-95	95-100
21 days	5	2	2.3	3.1	3.2	2.3	2.7	2.1	1.9	2.1	2.1	2.6
		5	2.1	3.1	2.9	1.9	2.9	2.3	2.5	2.5	2.7	2.7
35 days	0.25	2	2.8	2.2	3.5	1.9	3.3	2.3	3.0	2.4	2.3	3.0
		5	2.9	2.2	2.6	2.6	2.1	3.1	3.0	3.0	2.5	1.5
		10	3.1	2.5	2.7	3.2	2.5	3.4	3.2	2.4	3.1	2.7
	1	2	2.7	2.7	2.1	2.5	2.8	2.3	2.5	3.0	2.7	2.1
		5	2.1	2.7	3.0	2.1	2.6	2.9	3.0	1.9	2.5	2.6
		10	2.5	3.2	1.7	2.4	2.9	2.6	3.1	2.7	2.5	2.5
	5	2	2.5	2.3	3.8	2.3	2.7	2.9	2.6	2.2	2.7	2.5
		5	3.1	2.0	2.6	2.0	3.1	2.8	2.1	2.3	2.6	2.7

APPENDIX 3

WATER-DEPRIVATION EXPERIMENTS

Seconds Reward/ Trial	Number of days Deprived	Number of Trials/Day	MEAN NO. OF ERRORS FOR GROUPS OF 5 ANIMALS OVER BLOCKS OF FIVE TRIALS									
			TRIALS IN GROUPS OF FIVE									
			1-5	5-10	10-15	15-20	20-25	25-30	30-35	35-40	40-45	45-50
	14	2	2.5	2.3	2.7	2.3	2.7	2.8	2.9	1.8	2.3	2.8
		5	3.9	2.6	2.0	3.8	2.5	3.2	2.8	3.6	1.9	2.8
	21	2	3.0	2.8	2.3	3.9	2.4	1.8	3.1	3.5	4.2	3.0
		5	2.2	2.0	2.8	1.8	2.5	2.2	2.2	1.4	2.6	3.8
	28	2	2.3	2.8	2.4	3.2	1.8	2.8	2.3	1.8	3.5	3.2
		5	3.0	3.0	2.6	3.1	2.4	3.0	2.5	3.3	2.9	3.9
	14	2	2.1	1.9	2.6	1.2	2.3	2.0	2.0	1.9	2.2	2.5
		5	2.5	1.5	1.9	2.3	2.7	4.2	2.6	2.5	1.4	2.3
	21	2	2.3	2.5	2.5	2.9	3.0	2.5	1.4	2.4	2.6	2.4
		5	1.8	1.9	1.8	2.3	1.9	4.2	2.0	2.8	1.1	1.7
	28	2	2.5	3.2	2.3	2.5	3.4	2.6	1.9	2.2	2.3	2.5
		5	2.1	2.3	1.9	2.5	2.1	1.6	2.9	3.4	2.1	1.9

APPENDIX 3 (Cont'd)

WATER-DEPRIVATION EXPERIMENTS (Cont'd)

Seconds Reward/ Trial	Number of days Deprived	Number of Trials/Day	MEAN NO. OF ERRORS FOR GROUPS OF 5 ANIMALS OVER BLOCKS OF FIVE TRIALS									
			TRIALS IN GROUPS OF FIVE									
			50-55	55-60	60-65	65-70	70-75	75-80	80-85	85-90	90-95	95-100
10 secs/trial	14	2	1.9	2.6	1.7	2.7	2.4	2.8	4.2	2.3	1.9	3.7
		5	1.7	2.3	2.1	2.0	2.3	2.9	3.6	2.0	2.6	2.9
	21	2	1.9	2.4	2.3	2.6	2.4	2.7	3.5	1.9	2.1	2.1
		5	2.5	3.1	2.7	2.0	2.9	2.1	2.1	2.8	2.8	2.3
	28	2	2.7	2.8	2.5	2.1	2.3	3.0	1.7	3.2	3.0	2.5
		5	2.0	2.3	2.5	2.1	2.2	2.1	2.0	2.1	2.1	1.9
40 secs/trial	14	2	2.2	2.0	2.2	1.9	2.2	2.1	2.5	2.5	2.5	1.9
		5	2.5	1.4	3.8	2.5	2.6	3.8	1.5	4.2	1.7	2.3
	21	2	2.9	2.3	2.7	1.8	2.2	2.1	2.2	2.4	2.5	1.4
		5	2.6	3.5	2.4	3.9	1.4	2.3	1.9	2.2	1.9	2.1
	28	2	4.2	2.1	2.3	2.1	2.0	2.2	3.3	2.7	2.5	2.2
		5	2.8	2.8	1.9	3.2	1.7	2.3	2.5	3.2	2.2	4.2

APPENDIX 4

ELECTRIC SHOCK AVOIDANCE (POSITIONAL DISCRIMINATION)

Errors for each individual against trials.

Trials		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Animal Number	1	1	1	0	1	0	0	1	1	0	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0
	2	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
	3	1	0	1	0	1	0	0	0	1	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
	4	0	1	1	1	0	1	1	0	1	1	0	1	1	1	0	1	1	0	1	1	0	0	1	0	1	1	0	1	0	1
	5	1	0	1	0	0	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
	6	1	1	1	1	1	0	1	1	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Percentage Errors for All Animals/ 3 Trials		67			39			39			33			44			27			17			28			22			11		

APPENDIX 5

SIMPLE AVOIDANCE LEARNING

Animal Number			Pre-Training Trials					Training Trials																Test Trials	
			1	2	3	4	5	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	1	2
	15 secs before shock	1								A				A		A	A			A	A			A	A	A			
		2							A	A	A	A	A	A			A	A		A	A	A	A	A	A		A		A
		3		A						A	A				A	A		A			A	A	A	A			A	
		4				A		A	A	A		A	A	A	A	A	A	A	A	A	A	A	A		A	A	A		A
		5							A		A	A	A				A	A	A		A	A	A	A	A	A	A		A
		6		A							A	A			A				A	A	A	A		A					
		7												A		A	A		A			A	A	A		A	A		A
		8	A							A		A			A		A	A	A		A	A	A		A	A	A		A
		9								A		A	A		A	A					A	A	A	A	A	A	A		A
		10							A			A		A				A		A	A		A			A			
	60 secs before shock	1							A	A	A	A	A	A	A		A	A	A	A	A	A	A			A	A		A
		2							A	A	A	A		A	A	A		A	A	A	A	A	A			A	A		A
		3		A					A	A		A	A	A	A	A	A	A	A	A	A			A		A	A		A
		4													A	A	A	A			A	A	A	A		A	A		
		5	A		A				A	A	A	A		A		A	A			A	A	A	A	A	A	A	A	A	A
		6						A	A	A	A	A	A	A	A			A		A	A	A		A	A	A	A		
		7		A					A				A	A	A	A	A		A	A	A	A	A	A	A	A	A		A
		8							A		A		A	A		A			A	A	A	A	A	A	A	A	A		A
		9							A	A			A	A	A	A	A		A	A	A	A	A	A	A	A			
		10				A			A			A				A			A	A	A		A	A		A			A

A - ANIMAL AVOIDED SHOCK

APPENDIX 6

AVOIDANCE LEARNING IN THE SHUTTLEBOX

A. ESCAPE DISTANCE in inches

Animal Number		ESCAPE DISTANCE IN INCHES AVERAGED FOR GROUPS OF 5 TRIALS																								
		Trials in Groups of Five																								
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
GROUP I	1	18	8	10	7	11	8	7	3	6	4	6	7	5	8	5	5	4	5	4	6	4	5	5	4	5
	2	28	16	12	8	11	6	6	7	12	7	8	9	8	8	8	7	5	6	5	4	4	5	6	4	7
	3	21	14	11	10	11	9	5	7	6	8	7	7	6	5	6	9	4	5	6	5	9	5	2	4	5
	4	24	12	10	10	9	13	10	7	12	7	7	6	4	6	8	4	3	5	5	5	7	4	4	2	5
	5	21	10	10	13	7	3	6	5	4	3	5	4	5	7	5	6	4	6	3	6	5	3	3	3	4
	6	20	14	10	7	7	8	6	7	12	8	8	5	4	7	6	3	7	4	4	5	3	6	3	5	4
	7	27	17	13	12	10	7	5	8	9	5	6	3	6	5	5	7	5	5	4	3	2	3	5	6	5
GROUP II	1	13	11	12	4	6	30	7	7	8	9	22	6	26	16	26	25	32								
	2	24	17	11	10	18	8	9	7	9	18	12	8	7	6	8	5	5	14	18	8	9	8	21	33	
	3	15	17	10	12	15	10	8	7	15	14	11	22	16	27											
	4	25	10	10	10	9	6	8	5	6	7	6	9	7	7	10	6	8	6	14	9	5	7	8	8	5
	5	19	11	16	7	11	22	8	7	26	23	31	13	10	30	28	32									

APPENDIX 6 (Cont'd)

AVOIDANCE LEARNING IN THE SHUTTLEBOX

A. ESCAPE DISTANCE in inches (Cont'd)

Animal Number		ESCAPE DISTANCE IN INCHES AVERAGED FOR GROUPS OF 5 TRIALS																									
		Trials in Groups of Five																									
		26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	
GROUP I	1	6	6	4	7	4	3	5	2	4	3	6	3	4	3	3	5	5	4	4	5	5	3	5	5	4	
	2	6	5	5	4	5	6	4	4	3	2	5	5	3	5	4	4	6	5	3	6	4	3	4	5	4	
	3	4	3	4	5	5	5	4	5	4	2	5	4	4	5	4	4	4	5	8	3	4	4	4	4	4	
	4	7	5	5	5	4	5	4	5	3	4	4	3	3	5	5	4	3	6	5	4	4	3	5	2		
	5	4	6	4	3	4	5	2	3	4	5	5	4	6	5	4	5	5	4	2	3	4	5	6	4	5	
	6	4	4	5	4	6	5	2	5	3	5	4	5	3	7	3	5	2	4	4	6	5	4	4	4	5	
	7	3	4	5	4	5	6	4	7	4	3	2	5	5	4	4	3	6	4	2	4	4	5	2	3	3	
GROUP II	1																										
	2																										
	3																										
	4	6	12	8	22	29																					
	5																										

APPENDIX 6 (Cont'd)

B. BEHAVIOURAL SCORES

AVERAGE PERCENTAGE OCCURRENCE FOR GROUPS OF ANIMALS/TEN TRIALS

		GROUPS OF TEN TRIALS																								
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
GROUP ONE	Re-entry	27	9	3	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Turn	11	21	21	17	7	10	4	6	4	9	4	4	6	6	6	7	1	1	-	4	4	3	6	4	3
	Approach	-	1	3	13	19	13	16	26	24	21	21	26	23	31	37	34	41	41	43	43	34	36	43	44	40
	Near	-	-	-	10	11	13	34	17	27	41	28	21	23	36	34	36	45	30	36	27	34	30	36	27	34
	Spont. Crossing	9	16	11	21	13	20	16	19	23	17	14	25	27	28	28	29	29	30	30	27	30	30	29	32	33
	Continue	-	-	1	1	4	4	4	6	11	8	10	10	11	7	10	9	11	9	7	10	9	10	10	10	10
	Refuse	-	-	3	3	4	3	4	-	6	-	3	3	-	3	1	1	-	1	3	-	1	3	-	1	1
	Postural	3	7	9	4	13	8	4	9	7	7	6	10	7	9	6	6	10	6	6	6	6	4	4	3	7
GROUP TWO	Re-entry	26	8	10	-	10	8	14	20	13	-	-	15	-	-	40										
	Turn	6	26	10	8	8	6	2	12	12	15	25	10	30	-	-										
	Spont. Crossing	4	18	2	8	14	16	24	19	18	5	10	15	30	40	40										
	Refuse	-	-	18	2	16	22	18	27	23	20	25	40	-	20	60										
	Postural Avoidance	8	6	16	8	12	18	10	22	7	10	2	20	5	5	60										

APPENDIX 7

DISCRIMINATION OF SINGLE CUES

	AVERAGE ERRORS FOR GROUPS OF 5 ANIMALS OVER BLOCKS OF FIVE TRIALS													
	TRIALS IN GROUPS OF FIVE													
	Learning													
STIMULI	1	2	3	4	5	6	7	8	9	10	11	12		
Air Currents	2.6	2.4	2.6	1.7	1.5	1.0	1.5	0	0	—	—	—		
Light/Dark	2.6	3.2	2.4	1.6	1.8	1.6	1.6	1.2	2.0	1.0	1.0	0.0		
Odour	3.0	2.4	2.0	2.0	2.0	1.0	1.4	2.0	0.0	2.0	0.0	1.0		
					Re-Learning									
STIMULI	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Air Currents	3.8	2.4	0.8	1.7	1.7	2.5	2.0	1.0	0.0	2.0	0.0	2.0	0.0	1.0
Light/Dark	3.2	2.4	3.0	1.7	1.5	2.0	0.7	1.0	1.0	0.0	1.0	0.0	—	—
Odour	3.4	2.2	2.2	1.5	1.2	0.0	1.5	0.0	1.0	—	—	—	—	—

APPENDIX 8A

REVERSAL LEARNING AND CONDITIONAL REVERSAL LEARNING

		NUMBER OF ERRORS TO CRITERION																								
	Animal Number	Reversal Number																								
		0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
REVERSAL GROUP	1	7	11	15	10	8	9	8	9	7	6	5	5	6	5	4	6	4	5	4	3	3	6	6	5
	2	20	14	11	9	9	9	9	6	6	6	6	6	6	7	5	7	5	4	5	5	5	4	8	7
	3	11	14	10	11	9	7	6	9	8	7	4	5	5	3	5	5	5	3	6	4	5	6	4	5
	4	14	10	9	9	5	7	10	7	6	9	4	6	5	6	4	5	4	5	6	5	6	4	5	4
	5	9	11	13	10	9	11	7	7	8	6	7	4	4	4	5	3	5	4	4	5	7	5	5	6
	6	13	11	10	8	9	7	5	8	7	8	5	5	7	5	6	7	6	5	7	3	4	5	4	4
CONTROL GROUP	1	TRAINED ON ONE OPTION																	14	9	5	5	7	7	7
	2																		16	11	7	6	5	6	3
	3																		16	10	5	7	5	5	5
	4																		12	7	4	5	4	4	4
	5																		15	7	4	5	5	5	3
	6																		21	10	6	5	8	8	6
CONDITIONAL REVERSAL GROUP	1	11	21	10	18	14	17	15	13	9	8	5	8	4	6	5	5	6	8	5	4	5	4	4	8
	2	21	20	15	15	7	12	18	9	8	12	8	6	5	6	6	6	4	6	4	7	6	6	5	5
	3	15	16	17	9	16	8	6	7	6	6	7	5	5	6	5	5	6	7	7	4	4	4	5	6
	4	9	20	14	12	13	7	10	6	8	6	6	5	4	5	5	6	7	5	4	5	5	5	6	2
	5	10	16	19	15	18	15	7	12	10	11	7	7	6	5	7	6	6	6	6	6	4	5	4	7
	6	13	19	13	13	19	8	19	11	9	6	6	8	6	4	6	5	7	6	5	7	5	6	5	5

APPENDIX 8B

REVERSAL LEARNING AND CONDITIONAL REVERSAL LEARNING

		% ERRORS FOR GROUPS OF SIX ANIMALS OVER THREE TRIAL BLOCKS														
			Number of trials in groups of three													
			1	2	3	4	5	6	7	8	9	10	11	12	13	14
REVERSAL GROUP	Reversal Number	0	50	50	38	44	28	33	26	33	20	28	25	11		
		1	67	61	44	33	33	33	39	22	17	25	17			
		10	84	28	33	22	0									
		23	78	50	28	6	6									
CONDITIONAL REVERSAL GROUP	Reversal Number	0	50	44	39	55	53	39	28	28	39	28	18			
		1	67	61	61	44	55	50	39	44	39	39	22	28	28	17
		10	78	33	44	28	11	18								
		23	67	55	33	6										
CONTROL GROUP	Reversal Number	1	95	55	61	44	39	55	28	33	28	11	19			
		6	61	17	22	8										

APPENDIX 9

AVOIDANCE LEARNING IN A NATURAL SITUATION

		% TIME SPENT IN CENTRAL AREA IN EACH OBSERVATION PERIOD																	
		OBSERVATION PERIODS																	
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Animal Number GROUP ONE	1	15	30	25	45	100	85	100	95	100									
	2	15	45	10	20	0	0	0	0	0	0	10	100	100	85	100	95	100	100
	3	5	15	0	0	5*	0	0	0	0	0	0	5	0	0	0	5*	0	0
	4	0	100	10	0	0	0	5	0	5	0	25	85	0	5	0	0	5*	0
	5	15	0	40	0	0	5	0	0	0	5*	15	100	0	0	0	0	15	0
	6	15	100	0	5*	0	0	5	0	0	0	25	5	0	0	0	5	5	0
	7	20	60	40	0	0	0	10	0	5*	5	40	15	5*	10	0	10	0	0
	8	60	20	0	0	5	0	0	0	0	0	10	0	0	0	5	0	0	0
	9	10	20	35	0	0	5*	0	0	10	0	0	0	0	0	0	0	5	0
	10	0	0	5	0	0	0	0	0	0	0	5	25	0	15	25	0	5*	5

APPENDIX 9 (Cont'd)

AVOIDANCE LEARNING IN A NATURAL SITUATION (Cont'd)

		% TIME SPENT IN CENTRAL AREA IN EACH OBSERVATION PERIOD															
		OBSERVATION PERIODS															
		19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
Animal Number GROUP ONE	1																	
	2																	
	3	5	40	25	100	100	100	95	100	100								
	4	0	15	45	15	0	5	0	0	0	0	25	25	15	55	100	85	100
	5	5	30	100	0	5	0	5	0	0	5	35	65	75	10	5*	0	0
	6	0	25	30	5	0	0	0	10	0	0	35	5	0	0	5	0	5
	7	5	10	20	10	0	5	0	0	0	5	0	25	5	5*	0	5	0
	8	5*	15	100	5	5	0	0	15	0	0	100	5	0	0	10	0	5*
	9	0	0	40	0	5	5*	5	0	0	5*	15	45	5	10	0	5	0
	10	15	100	100	15	5*	25	15	25	5	5	85	100	0	0	5	5	5

APPENDIX 9 (Cont'd)

AVOIDANCE LEARNING IN A NATURAL SITUATION (Cont'd)

		% TIME SPENT IN CENTRAL AREA IN EACH OBSERVATION PERIOD																	
		OBSERVATION PERIODS																	
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Animal Number GROUP TWO	1	20	0	100	100	85	100	95	100	100									
	2	0	5	0	0	0	0	0	0	0	0	0	0	65	90	100	95	100	90
	3	35	55	10	0	0	0	0	0	0	0	0	5	0	0	0	0	5*	5
	4	40	5	0	5	5	0	0	70	5	5*	0	0	0	0	0	0	0	0
	5	15	0	5	0	10	20	0	5	0	0	10	10	0	0	0	5*	0	0
	6	30	85	5	5*	10	5	0	10	85	0	35	60	0	0	5*	0	0	5
	7	15	5	0	0	0	0	5	0	0	0	10	5	0	5*	0	0	5	0
	8	5	15	0	5	0	10	0	0	5*	0	45	0	15	0	0	10	0	10
	9	0	0	0	0	0	0	0	0	0	0	0	10	0	0	5	0	0	5
	10	5	0	0	0	0	0	5*	0	0	0	5	5	0	0	0	0	0	0

APPENDIX 9 (Cont'd)

AVOIDANCE LEARNING IN A NATURAL SITUATION (Cont'd)

		% TIME SPENT IN CENTRAL AREA IN EACH OBSERVATION PERIOD																
		OBSERVATION PERIODS																
		19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
Animal Number GROUP TWO	1																	
	2																	
	3	0	15	30	100	95	85	100	100	100	0	10	65	95	100	85	95	100
	4	0	0	40	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	5	0	0	15	15	0	15	10	0	10	0	15	0	0	0	0	0	0
	6	0	0	35	10	40	0	5*	0	5	0	0	100	0	5*	0	5	0
	7	0	5	0	0	10	0	0	0	0	5	0	15	5	0	0	0	5*
	8	5	15	35	10	5*	5	0	5*	0	5	10	100	0	5	0	0	5
	9	0	10	5	5	10	0	5	0	0	0	0	15	5*	0	0	5*	0
	10	0	5	0	0	0	0	0	0	0	0	100	0	0	0	0	0	0

APPENDIX 9b

Experiments in a semi-natural situation.

GROUP ONE. Fights between the dominant and all the subordinate animals.

Observation periods.

Animal number.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
1	Dominant.																																		
2	0	XX X	X	2X	-	-	-	-	-	Dominant.																									
3	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	Dominant.															
4	-	-	X	-	-	-	-	-	X	-	-	XX	-	X	-	-	-	-	-	-	XX 5X	X	-	-	-	-	-	Dominant						
5	XX 2X	-	3X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	X	-	-	-	0	X	-	-	-	-
6	XX	XX	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	X	-	-	-	-	-	-	-	0	-	-	-	-	-
7	X	3X	2X	-	-	-	X	-	-	-	-	X	-	2X	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	X	-	-	X	-
8	5X	-	-	-	X	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-
9	-	X	3X	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	X	-	-	-	X	-	-	-	X	-
10	-	-	X	-	-	-	-	-	-	-	-	X	-	2X	-	-	-	-	-	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-

0- dominant loses.
XX - dominant wins
X - dominant chases other animal away.
- no fight occurs.

APPENDIX 10

PRELIMINARY EXPERIMENTS

Animal Number	NUMBER OF ERRORS/TRIAL													
	TRIALS													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1	0	0	0	0	0	0	0	0	0	0				
2	1	0	0	0	0	0	1	0	0	0	0			
3	1	0	1	0	0	0	0	0	0	0	0			
4	0	1	0	1	1	0	0	0	0	0	0	0	0	0
5	1	0	0	0	0	0	0	0	0					
6	0	0	0	1	0	0	0	0	0					

APPENDIX 11A

REVERSAL LEARNING AND CONDITIONAL REVERSAL LEARNING

		ERRORS TO CRITERION										
		Reversal Number										
	Animal Number	0	1	2	3	4	5	6	7	8	9	10
REVERSAL GROUP	1	2	2	3	7	4	5	7	10	4	9	11
	2	1	3	4	4	6	7	6	8	8	9	9
	3	3	1	3	3	6	6	4	7	9	10	12
	4	1	4	2	5	4	3	5	7	8	7	7
	5	2	3	6	5	5	5	8	6	9	14	8
	6	4	2	4	4	3	4	8	6	4	9	12
	7	1	2	3	4	5	5	6	10	12	7	11
	8	1	4	3	4	7	4	5	9	5	11	6
CONDITIONAL REVERSAL GROUP	1	2	2	4	4	3	6	8	7	11	13	10
	2	3	2	5	6	6	4	8	9	9	6	8
	3	2	4	4	2	5	5	5	7	7	10	9
	4	2	3	1	3	3	4	6	8	10	7	11
	5	2	3	4	4	6	4	5	6	9	21	6
	6	2	1	2	3	5	6	6	4	6	8	7
	7	2	2	2	2	5	5	4	8	6	8	7
	8	2	3	2	4	3	4	6	9	7	10	7

APPENDIX 11 B

REVERSAL LEARNING AND CONDITIONAL REVERSAL LEARNING

		AVERAGE % ERRORS FOR GROUPS OF EIGHT ANIMALS																												
		Trials																												
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
REVERSAL GROUP	0	62	37	37	37	25	0	12	0	12	0	0	0																	
	5	100	25	50	25	50	50	12	62	37	25	25	12	0	0	14	0	0	0	0										
	10	100	50	37	50	50	37	25	37	62	12	62	37	25	50	12	37	37	37	37	37	25	12	12	12	0	0	0		
CONDITIONAL REVERSAL GROUP	0	50	50	37	0	25	12	0	25	0	0	0																		
	5	87	37	50	37	37	50	12	12	50	0	25	25	12	0	17	17	0	0											
	10	100	37	50	25	50	50	37	37	37	37	50	37	25	25	37	25	12	25	25	12	0	25	12	14	0	33	0	0	0

APPENDIX 11 C

REVERSAL LEARNING

	NUMBER OF ERRORS FOR ONE INDIVIDUAL																														
	Trials																														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
REVERSAL NUMBER 0	1	0	0	1	0	0	0	0	0	0	0																				
REVERSAL NUMBER 5	1	0	1	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0													
REVERSAL NUMBER 10	1	1	1	0	1	1	0	0	1	0	1	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0

APPENDIX 12

THE CONCEPT OF 'TRIANGULARITY'

FINAL SERIES OF UNREWARDED DISCRIMINATION TESTS

Figure Pairs	TOTAL NUMBER OF APPROACHES TO EACH FIGURE		
	Experiment One	Experiment Two	Experiment Three
13	311	368	294
16	109	123	43
8	262	309	278
9	44	68	81
17	247	323	372
20	32	99	67
13	204	225	133
16	238	208	145
8	169	280	108
9	178	296	101
17	221	207	162
20	242	188	184
8	209	364	293
9	44	97	161
17	296	381	247
20	39	60	70

STATISTICAL APPENDIX I.

Regression Analysis.

The fitted regression line is given by the formula

$$y = a + bx$$

where the regression coefficient b

$$b = \frac{\sum(x - \bar{x}) (y - \bar{y})}{\sum(x - \bar{x})^2}$$

x and y are a series of paired values of results and $\bar{x}$ and $\bar{y}$ represent their mean values.

The constant a is estimated by

$$a = \bar{y} - b\bar{x}$$

One Sample Runs Test.

From the above fitted regression line it is possible to calculate the expected value of y for any value of x. The experimental value of y for each individual trial is compared with the expected value and is classified as + or - according to whether it lies above or below this value. The sequential order of + and - values is then examined. Below is shown the order of + and - values for the 85 trials given to Animal 1 (see figure fourteen B).

```
   1  /2//4 ///7/    8    / 9  /     10        / ///// 16 /
+++++ +-+-- +-+++ ----- -----+ +++++ ----- ----- ----- +-+-+ -----/
17 ///20 /// //25/ // /  29  /
+++-+ ---+- +-+++ -+--+ +++++
```

From this sequence is calculated

n1 = the number of + signs.

n2 = the number of - signs.

r = the number of runs.

A run is a succession of identical symbols. In the example above the runs are marked by / signs and numbered up to 29, the total number of runs in this case. A test is now performed to see whether the number of runs differs from that of a random sample, the prediction being that there will be less than the random number of runs.

The value of z is calculated by the formula :-

$$z = \frac{r - \left(\frac{2.n1.n2.}{n1 + n2} + 1 \right)}{\sqrt{\frac{2.n1.n2.(2.n1.n2. - n1 - n2)}{(n1 + n2)^2 (n1 + n2 - 1)}}}$$

z is a normally distributed variable with zero mean and unit variance and the significance of any observed value of z computed from this formula may be determined by reference to a normal curve table.

In the example above, animal 1, $z = -2.9691$ and $p = 0.0015$.

STATISTICAL APPENDIX II.

Regression lines are calculated for each set of results (see statistical appendix I). The variance about each regression line is then calculated by the formula

$$s^2 = \frac{1}{n-2}\left\{\Sigma(y-\bar{y})^2 - \frac{\left[\Sigma(x-\bar{x})(y-\bar{y})\right]^2}{(x-\bar{x})^2}\right\}$$

where x and y are a number of pairs of results, n the number of observations and $\bar{x}$ and $\bar{y}$ the mean values of x and y.

It is then possible to estimate the standard error of the regression coefficients by the formula

$$\text{standard error} = \frac{s}{\sqrt{\Sigma(x-\bar{x})^2}}$$

It is now easy to compare the two regression coefficients as they may be regarded as normally distributed estimates of known mean and standard error. d is calculated by the formula

$$d = \frac{b1 - b2}{\sqrt{\frac{s1^2}{\Sigma1\,(x-\bar{x}1)^2} + \frac{s2^2}{\Sigma2\,(x-x2)^2}}}$$

where the suffixes 1 and 2 refer to the two sets of data. d is normally distributed with zero mean and unit standard deviation and the significance of an observed value of d is computed by reference to a normal curve table.